

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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(Continued on inside back cover)

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The Biology of the Mussel Crab, *Fabia subquadrata*, from the Waters of the San Juan Archipelago, Washington

JACK B. PEARCE¹

THE MUSSEL CRAB, *Fabia subquadrata*, described by Dana in 1851 from material collected in Puget Sound, is placed in the subfamily Pinnotherinae Milne-Edwards, one of the two subfamilies of the Pinnotheridae indigenous to the Americas.

Most species of pinnotherids live in association with a host organism. The relationships have been variously described as parasitism, commensalism, or mutualism. Although the mussel crab is usually found in association with the horse mussel, *Modiolus modiolus*, several other pelecypod hosts as well as a tunicate have been reported (Wells, 1928:289). The present research has revealed additional bivalve host species. It is frequently reported from both species of *Mytilus* in waters south of Puget Sound, although in the latter waters it does not appear to frequent these hosts.

The life cycle of *F. subquadrata* is complex and, as with many pinnotherids, includes several developmental forms subsequent to the typical decapod larval stages (i.e., the zoea and megalops) and before the definitive adult stage is reached. As in most marine decapods, the early pinnotherid zoea and megalops are planktonic. Upon moulting from the megalops into the first true crab stage the animal, it is thought, leaves the plankton and becomes associated with its host.

Postplanktonic developmental stages of a pinnotherid were first described by Atkins (1926:475) for *Pinnotheres pisum*, which is common to the coast of the British Isles. Later Stauber (1945:269) found that the developmental cycle of the North American east coast pinnotherid, *Pinnotheres ostreum*, was very much the same as that previously described for *P. pisum*. The re-

sults of the present study indicate that *F. subquadrata* passes through stages comparable to those reported for *P. pisum* by Atkins and *P. ostreum* by Stauber and by Christensen and McDermott (1958:150). There are, however, important differences in the developmental cycle of *P. subquadrata*.

The present known range of the mussel crab is from the coast of Alaska to southern California. Rathbun (1918:102) noted it in waters 250 m deep and Wells (1940:47) found it in mussels dredged at a depth of 220 m. Hart (personal communication) has found it in *M. modiolus* taken intertidally near Victoria, Vancouver Island, British Columbia.

While it is true that pinnotherid crabs have been known from ancient times, only recently have there been any comprehensive studies of any member of this family. Atkins's early observations (1926) on the moulting stages of *P. pisum* laid the groundwork for future studies. This was followed by Hart's investigations (1935) in which she reported success in hatching the eggs of *Pinnotheres taylori* and rearing them through the first true crab stage. Sandoz and Hopkins (1947:250) were able to rear *P. ostreum* to this same stage. These investigations extended the earlier work of Atkins, in which the hard and posthard stages subsequent to the first crab stage had been described. Atkins (1955) later raised two species of British pinnotherids, *P. pisum* and *P. pinnotheres*, through the megalops stage.

Most of the workers cited above were concerned largely with the early development of the crabs rather than with their ecology or association with the hosts. Wells' studies (1928, 1940) were among the first published papers concerned with the biology of American species of pinnotherids. Later Stauber (1945) investigated the postlarval development and habits of the oyster crab, *P. ostreum*. This work was followed by that of Christensen and McDermott (1958) which

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represents the most comprehensive study of this or any other species of the Pinnotheridae.

Except for purely taxonomic studies, these papers are the main reports concerning the pinnotherids despite Rathbun's (1918:10) early admonishment concerning the lack of knowledge of this family and the inherent rewards to be found in its study.

Other than Wells' data (1928, 1940) there have been no extensive reports concerning the biology of *F. subquadrata*. It is, therefore, one of the least studied species of the Pinnotheridae. Until Wells' work of 1928 the male of the species had not been recognized and was, in fact, described as a separate species in a different genus, *Pinnotheres concharum*.

The present paper is concerned with the biology of this neglected species. The principal study was conducted over a period of one and one-half years, from June, 1958 to January, 1960, but many observations made subsequent to the main investigation have been incorporated in this paper. Information on the developmental cycle, reproductive biology, relationship to the host organism, distribution and size in relation to water depth, and ecdysis is reported here.

The author is especially indebted to Dr. Dixy L. Ray, as well as to Dr. Robert Fernald, Dr. Ernst Florey, and Dr. Paul Illg, whose valuable assistance and helpful criticisms were most useful in the preparation of this paper. The many valuable suggestions of Dr. J. F. L. Hart of Victoria, British Columbia, and the critical reading of the manuscript by A. M. Christensen are also acknowledged.

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MATERIALS AND METHODS

All field work involved in this study was carried out at the Marine Laboratory of the Uni-

versity of Washington, Friday Harbor, San Juan Island, Washington. Observations were made on the contents of host mussels collected at least once but frequently twice per month throughout the period of study. In addition, materials were collected once a week during the summer of June, July, and August of 1958 and 1959. A total of 3,480 host mussels were examined during this period.

The mussels were collected by dredging in localities where they are known to occur. The dredging gear included either a standard rock dredge or beam trawl, depending upon the type of bottom from which the mussels were to be removed.

Several areas within the San Juan Archipelago, selected as dredging sites, were chosen as being representative of a variety of depths and bottom types. The deepest stations were located in President Channel northwest of Orcas Island ($48^{\circ}39'45''\text{N}$, $123^{\circ}1'\text{W}$), where the water is 195 m in depth. The shallowest station is off Point Lawrence, Orcas Island ($48^{\circ}39'30''\text{N}$, $122^{\circ}44'45''\text{W}$), where the water is 22–30 m in depth. Other stations were located near Point Caution, San Juan Island ($48^{\circ}34'\text{N}$, $123^{\circ}0'48''\text{W}$) in water 130 m in depth; off Mineral Point, San Juan Island ($48^{\circ}35'10''\text{N}$, $123^{\circ}3'35''\text{W}$) in waters 55 and 130 m deep; and in East Pea Vine Pass ($48^{\circ}35'30''\text{N}$, $122^{\circ}47'30''\text{W}$) in 48 m of water.

Upon being brought to the surface the mussels were immediately placed in live boxes with circulating sea water. The drains of these boxes are covered with screening of a gauge sufficient to insure that any swimming stage crabs would be retained should they leave their hosts. The mussels were then brought into the laboratory where they were opened and examined alive for the presence of crabs. In those mussels that were infested, any damage which may have occurred as a result of a crab's presence was noted. A dissecting microscope was always used in these examinations. Each mussel was measured, the larger ones (greater than 10 mm in length) with a vernier caliper, the smaller with a dial caliper. The larger mussels were measured to the nearest 0.5 mm, the smaller (less than 10 mm) to 0.1 mm. All crabs collected after July 15, 1958 were measured with an ocular microm-

eter to the nearest 0.01 mm. The greatest width of both carapace and abdomen were noted.

The crabs were then placed in standard household polyethylene ice cube trays. Each tray consists of 14 cubicles and 1 crab was held in each of these. A "vaporite" pen was used to number each cubicle with the crab's respective catalog number. In this manner several hundred crabs could be retained, facilitating observations on their behavior, ecdysis, and subsequent changes. The crabs were kept at temperatures approximating those of their natural environment, and either a flow of water from the sea water system or several daily changes were used to maintain adequate environmental conditions.

DEVELOPMENTAL STAGES IN *F. subquadrata*

As previously noted the life cycle of *F. subquadrata* is similar to that described for *P. pisum* (Atkins, 1926:475) and *P. ostreum* (Stauber, 1945:272; Christensen and McDermott, 1958:150). The typical planktonic zoeal and megalopal stages are followed by a series of true crab instars. The first of these is the invasive crab (Christensen and McDermott, 1958:150). Following the invasion of the host organism several instars occur which are collectively designated as *prehard stages*. These prehard crabs have a soft, membranous exoskeleton. With the exception of the initial invasive stage there is little setal ornamentation on the pereopods, which are cylindrical in shape.

While the prehard instars were thought to occur they were not described for any pinnotherid until the investigation of *P. ostreum* by Christensen and McDermott (1958:147). The total number of prehard instars is still not known for any species, although Hart (personal communication) has found up to five prehard instars in *F. subquadrata*. Since the terminal one of these is smaller than the smallest Stage I crabs of this species it is certain that at least seven prehard instars normally occur between the megalops and the Stage I crab. Because there is a considerable variation in the size of the terminal prehard instar it may be assumed that the total number of prehard instars also varies somewhat.

Subsequent to the series of prehard crab

stages a very anomalous instar appears. First described by Atkins (1926:478) for *P. pisum* as the Stage I crab, this instar is, in its morphology and behavior, entirely different from any of the stages preceding or following it. The exoskeleton is well calcified and very hard. It is, in many species, highly pigmented with definite patterns on the carapace. Above all it is highly modified for a temporary, freeswimming planktonic existence. The setal ornamentation found on the pereopods is extensive and, in addition, these appendages are broad and flattened in contrast to the cylindrical condition noted in the prehard instars. They thus serve as very effective swimming appendages. It has been reported for *P. pisum* (Atkins, 1926:475) and *P. ostreum* (Stauber, 1945:272; Christensen and McDermott, 1958:152) that at this stage of development the males leave their host to seek out females, copulating with them in their host.

To this point of development the male and female crabs have paralleled each other. The external morphology of both sexes is very similar throughout the prehard series and the Stage I instar. Only by the examination of the external genitalia can the two sexes be distinguished.

Following this stage a dichotomy occurs in the developmental cycle of the two sexes. The male is thought to remain in the hard stage, dying after breeding. The female, however, moults soon after copulation and the new posthard instar is soft, with a membranous exoskeleton comparable to that of the earlier prehard stages. The first posthard stage is referred to as the Stage II female. It is followed, both in *P. pisum* and *P. ostreum*, by Stages III, IV, and V. These stages are characterized by an overall increase in size, greater complexity of the pleopods, and an increase in the width of the abdomen relative to the carapace width. The Stage V crab is the terminal adult female. Although subsequent moults may occur, they result largely in an increase in size and there is little morphological change.

The Stage II crab is very similar in appearance to the terminal prehard instar. In *F. subquadrata* there is little increase in carapace or abdomen width during the terminal prehard–Stage I and Stage I–Stage II moults. This stage (II) is very difficult to identify unless the actual Stage I–

Stage II moult is observed. Stages following it can be readily distinguished, however, on the basis of the differential growth of the abdomen and increased complexity of the pleopods.

Since Atkins (1926:475) recognized only the Stage I-Stage V crabs and did not describe the prehard series, the nomenclature originally applied by her to the pinnotherid developmental instars is no longer adequate. However, as all the prehard stages have not been described for any pinnotherid crab it would be difficult to rename or renumber these forms at this time. For this reason her original terminology, with some modifications made by Christensen and McDermott (1958), has been retained in this investigation.

Invasive and Prehard Stages

The carapace of the invasive first crab stage of *F. subquadrata* is more square in outline than are the later prehard stages, which tend to be ovoid in shape. The eyestalks and pereopods of the first crab stage are also proportionately larger in relation to the rest of the body than are those of succeeding prehard instars. The pereopods of this instar are covered with swimming hairs or setae. The distributional pattern of these hairs is different, however, from that of the Stage I or hard crab, which also has similar setae. The pereopods of the first crab stage occur with the hairs distributed over much of the surface, giving the appendage a bottle-brush appearance. The hairs of this stage are also much more sparse and the entire structure does not appear to be as efficient an arrangement for swimming as that of the pereopods of the Stage I crab. Since the first stage crab apparently seeks out or in some manner becomes associated with a host immediately after moulting from the megalops, appendages well adapted to extended swimming activities are not necessary. This instar is able to swim, however, as is demonstrated by its activities in the laboratory.

As an individual crab progresses through the series of prehard moults the swimming hairs found on the pereopods, as well as the swimming abilities and activity, are lost until the Stage I or hard instar is attained. At this point the swimming hairs, as well as the general mor-

phology, become highly modified. The significance of this sudden transformation is discussed in a later portion of this paper.

The pleopods of the first crab stage and the first few prehard instars subsequent to it are merely small knobs protruding from the ventral surface of the abdomen. At this time there is no differentiation into endo- or exopodites. In the later prehard instars immediately preceding the Stage I or hard instar, the pleopods become very conspicuous and show clear differentiation into endo- and exopodite portions.

The smallest *F. subquadrata* found within a mussel measured 0.85 mm in carapace width. This crab is somewhat larger than the first crab stage of this species reared by Hart (personal communication), which had a carapace width of 0.76 mm. This difference in size may be accounted for by assuming that the formerly planktonic first crab stage undergoes a moult very soon after entering the host mussel. Consequently it would be difficult to find a true first stage crab in a host mussel.

However, comparison of the supposed first crab stages removed from mussels with the known first crab stage raised by Hart indicates that morphologically they are very similar or identical.

As earlier noted, Hart has reared *F. subquadrata* through five prehard instars, the largest of these still being somewhat smaller than the smallest Stage I instar yet observed (1.3 mm). For this reason it may be suspected that several instars intervene between the aforementioned forms. Christensen and McDermott (1958:150) found that the smallest *P. ostreum* collected measured 0.59 mm. They suggested that at least four moults occur before a crab would moult into the Stage I instar. The smallest Stage I instar in their collection also measures 1.3 mm. Since, however, the Stage I *F. subquadrata* is normally somewhat larger, it is suspected that at least seven moults occur between the invasive first crab stage and the average Stage I instar. When the method used by Hiatt (1948:165) to extrapolate the number of intermolt periods in *Pachygrapsus crassipes* was applied to *F. subquadrata* it was confirmed that approximately seven to eight moults occurred between the first crab stage and the average size Stage I instar.

The abdomen width of the smallest *F. subquadrata* removed from a mussel was 0.26 mm or approximately one-third the carapace width. This is a ratio that is approximated in all developmental instars through the Stage II posthard. With the exception of a few abnormal females it is true for the hard Stage I form.

Apparently it is rare for a male Stage I *F. subquadrata* to moult into a posthard, soft carapace crab. As will be discussed later, however, such males do occasionally occur and, in fact, may be more common than suspected. In order to obtain an approximation of the size of the terminal prehard instars, both males and females, each individual collected was measured. If, within a week, the crab moulted into a Stage I instar the previous dimensions were recorded as those of a terminal prehard.

The carapace width of 19 male prehard crabs varied from 3.0–5.3 mm, with a mean width of 4.3 mm. The abdomen width ranged from 1.1–2.1 mm and averaged 1.7 mm. It should be kept in mind, however, that males may occasionally moult into a soft instar from the hard Stage I form. Furthermore, as will be discussed later, this soft instar may subsequently revert to the hard form. Such a moulting sequence may thus invalidate these measurements.

Since the female regularly moults from a terminal prehard form into the Stage I instar any dimensions of these forms can be accepted as valid. Thirteen such moults were observed and the individuals involved ranged from 2.7–5.1 mm in carapace width prior to the moult. The average carapace width of these terminal prehard females was 4.1 mm.

The Stage I (Hard) Crabs

This is one of the stages originally described for *P. pisum* by Atkins (1926:478) and subsequently applied to the comparable instar of *P. ostreum* by Stauber (1945:272–276). The latter suggested that it was during this stage that *P. ostreum* invaded its oyster host.

The Stage I instar of *F. subquadrata* is in many ways morphologically similar to the Stage I form in both *P. pisum* and *P. ostreum*. In all three species the exoskeleton is well calcified and very hard. The pereopods are flattened

and well ornamented with functional swimming hairs; in *F. subquadrata* and *P. ostreum* only the second and third pereopods bear the long plumose swimming hairs, whereas they are present on all the walking legs of *P. pisum* (Christensen and McDermott, 1958:152). While Darbishire (1900) is quoted (Christensen and McDermott, 1958:152) as stating that the Stage I *P. pisum* uses the third and fourth pereopods for swimming, in contrast with *P. ostreum* which uses the second and third, recent observations by Christensen (personal communication) confirm that *P. pisum* uses primarily the second and third pereopods, as does *F. subquadrata*.

The carapace of the Stage I *F. subquadrata*, like that of *P. pisum*, is quite convex. The surface of this structure has a distinct pattern of bright orange markings (see Maerz and Paul, 1930, plate 10, E-12). This pattern is very constant and is found in almost all Stage I crabs. The background is a brilliant white. The orange pattern tends to fade to a dull brown (Maerz and Paul, plate 13, G-11) some weeks after being removed from the host mussel. Other stages of this species, both pre- and posthard, do not present any indication of this pigmentation. Macroscopically the exoskeleton in these latter forms appears colorless, although microscopic examination reveals isolated black and red chromatophores. Finally, as reported for the comparable stage of *P. ostreum* by Christensen and McDermott (1958:152), the Stage I *F. subquadrata* was noted to have two cylindrical rods connecting the dorsal and ventral sides of the body. These structures, along with the already discussed exoskeletal rigidity, may be modifications for a freeswimming existence.

Finally, in addition to these differences, the Stage I *F. subquadrata* varies from the other stages in having a heavy pubescence along the antero-lateral margins of the carapace. This pubescence appears somewhat heavier in the male, but such differences are hard to quantitate.

The average carapace width of 54 male Stage I crabs, selected at random from collections made on July 29, 1959, is 4.1 mm, with a range of from 1.3–6.8 mm. The mean of 29 female Stage I crabs collected on the same date is 3.5 mm, with a range of 1.5–6.2 mm. This does not

appear to be as large a size difference between sexes as was found for *P. ostreum* by Christensen and McDermott (1958). In addition to a sexual dimorphism in size the Stage I crabs have other sexual differences. The abdomen of the female is different in shape from that of the male; the lateral margins of the male's abdomen are concave, whereas those of the female are straight. It has also been noted that an occasional Stage I female will have an abdomen which is relatively wider than the 1:3 abdomen-carapace ratio which is characteristic of most of the Stage I crabs, both male and female. Finally, the abdomen of the female bears four well developed pairs of pleopods which contrast markedly with the two pairs of highly modified reproductive appendages borne by the male.

Both the male and female Stage I crabs have much stouter chelipeds than either the pre- or posthard growth forms. The merus and carpus are heavier and both fingers of the chela are swollen.

As observed by Stauber (1945:274) in *P. ostreum*, the Stage I *F. subquadrata* possesses a locking mechanism whereby the abdomen may be secured in the sternal groove. On the fifth thoracic segments of the sternal groove there are pairs of antero-ventrally directed knobs. These knobs hook under shelves found on the opposing ventral surfaces of the abdomen in such a manner as to become securely locked when any attempt is made to lift forcibly the abdomen of the living crab. Consequently, whereas it is easy to displace the abdomen of the pre- and posthard instars it is very difficult to free the abdomen from the sternal groove in the Stage I crabs.

The reproductive appendages of the male Stage I mussel crab are very similar to those described for *P. ostreum* by Stauber (1945:276), and quite dissimilar from the reproductive appendages of *P. pisum* as described by Atkins (1926:476). Atkins described the first copulatory appendage of *P. pisum* as blade-like and hairy. Recent examination of preserved *P. pisum* material by the present author verified a considerable difference. While the appendages of *P. pisum* are broad with almost parallel margins, except for the distal one-fourth of its length

where tapering occurs, they are, in *P. ostreum* and *F. subquadrata*, slender and lanceolate.

The Stage II Females

There is no apparent increase in body size of this instar over the Stage I female. The average carapace width of seven Stage II female crabs which were observed to moult from the Stage I instar is 3.4 mm, with a range of 2.9–3.9 mm. The average abdomen width is 1.1 mm, with a range of 0.9–1.3 mm.

The exoskeleton of the Stage II crabs is soft and membranous, as is that of the prehard instars. There are few swimming setae or hairs to be found on the pereopods, nor is there any pubescence along the anterolateral carapace margins.

The appendages are subcylindrical, not flattened as in the Stage I instar. The carapace is ovoid; the angles of the subpentagonal carapace of the Stage I form have become rounded. It is during this stage that the lateral carapace sulci (one of the definitive characters of the genus; Rathbun, 1918:101) become pronounced. They appear faintly in the prehard stages and are hardly present at all in the Stage I instar. Wells (1928:289) notes that these sulci are present in the newly moulted Stage I crab but are lost with subsequent hardening. As previously noted, the typical pigmentation of the Stage I instars is lost in the Stage II forms.

Stauber (1945:275) indicates large differences between the pleopods of Stages I, II, and III in *P. ostreum*. Christensen and McDermott (1958:152) suggest that Stauber's series of Stage II crabs may have included some prehard individuals. At any rate, no such marked differences could be found between the pleopods of terminal prehards and Stages I, II, and III of *F. subquadrata*.

There is little or no widening of the abdomen relative to the carapace in the Stage II crab. The ratio between the two is approximately the same as that of the Stage I forms. The sternal groove remains deep and is only as wide as the abdomen. The locking mechanism which was present and functional in the Stage I crabs no longer operates. As was surmised by Stauber (1945:278) for *P. ostreum*, this may be due to

the diminished rigidity of the exoskeleton in the posthard instars.

The Stage III Females

This is the first stage subsequent to the Stage I instar in which there is an increase in carapace width over that of the preceding instar, the Stage II form. The average width of 41 Stage III females was 5.4 mm, with a range of 4.0–5.9 mm. This instar is also the first in which the abdomen is more than one-third as wide as the carapace. The average abdomen width of the above Stage III crabs was 3.6 mm. The range was 3.2–4.2 mm.

Except for the relatively wider abdomen and larger overall body size the Stage III crab is, externally, morphologically similar to the Stage II form. The carapace is soft and membranous, the pereopods are slender and subcylindrical and devoid of swimming hairs. The sternal groove, however, is shallower and the abdomen no longer lies within the confines of this depression. Rather, it extends both laterally and anteriorly beyond the borders of the groove. The pleopods are almost identical in both structure and setation with those of the Stage II instar.

The Stage IV Females

The average carapace width of 33 Stage IV crabs is 5.8 mm. They range in width from 5.3–6.1 mm. The average abdomen width of these crabs is 5.4 mm with a range of from 4.8–5.9 mm. This stage is not only larger than the Stage III instars but in addition obvious external changes indicate that it is sexually more mature than those stages which precede it. Ovaries containing large numbers of developing eggs were observed in 29% of the Stage IV crabs. Also, while no ovigerous Stage IV crabs have been noted, it is significant that at this time the pleopods undergo the greatest change since their initial appearance. These modifications in the pleopods involve changes in size, proportion, and setal decoration. This is in preparation for the deposition and attachment of eggs. Finally, the abdomen is now nearly as wide as the carapace and is more concave than in previous instars.

The Stage V Females

This is the definitive adult female crab and the stage most commonly found throughout the year. As in previous posthard forms the exoskeleton is membranous and, while the body shape is similar to the Stage IV crabs, the relatively large growth of the abdomen causes this instar to become very awkward in its movements, especially when compared with the earlier stages. The abdomen is as wide or wider than the carapace and normally it protrudes laterally beyond the coxopodites and anteriorly to the mouth parts.

There is a great deal of variability in this stage, especially in the size and width of the abdomen relative to the carapace. From observations made on moulting Stage V crabs it has been found that this stage consists of not just one instar, as is usually true in the previous stages, but rather of a series of growth instars, in which the general morphology remains the same but with each succeeding instar become somewhat larger than the one preceding. This results in a wide range of size within this one, arbitrarily designated stage. The smallest Stage V crab observed measured only 4 mm in carapace width, whereas several Stage V crabs were found to measure 14 mm. The average carapace width of all observed Stage V crabs (831) was 9.5 mm, and the average abdomen width was 10.3 mm.

Christensen and McDermott (1958:162) discuss the effect of the presence of *P. ostreum* in slow-growing spat. They suggest that, while the growth of the crab is retarded in such host oysters, the development is not affected to a similar extent. The data gathered on the *F. subquadrata*–*M. modiolus* relationship would suggest that a similar situation prevails. The very small, below average in size, Stage V *F. subquadrata* are usually found in relatively smaller host mussels. In a more recent study Houghton (1963:254) reports a similar situation for *P. pisum*.

In addition to a positive correlation between crab and host size it has been determined that there is a negative correlation between the size of the Stage V crabs and the depth of the water from which they were removed. Crabs reaching

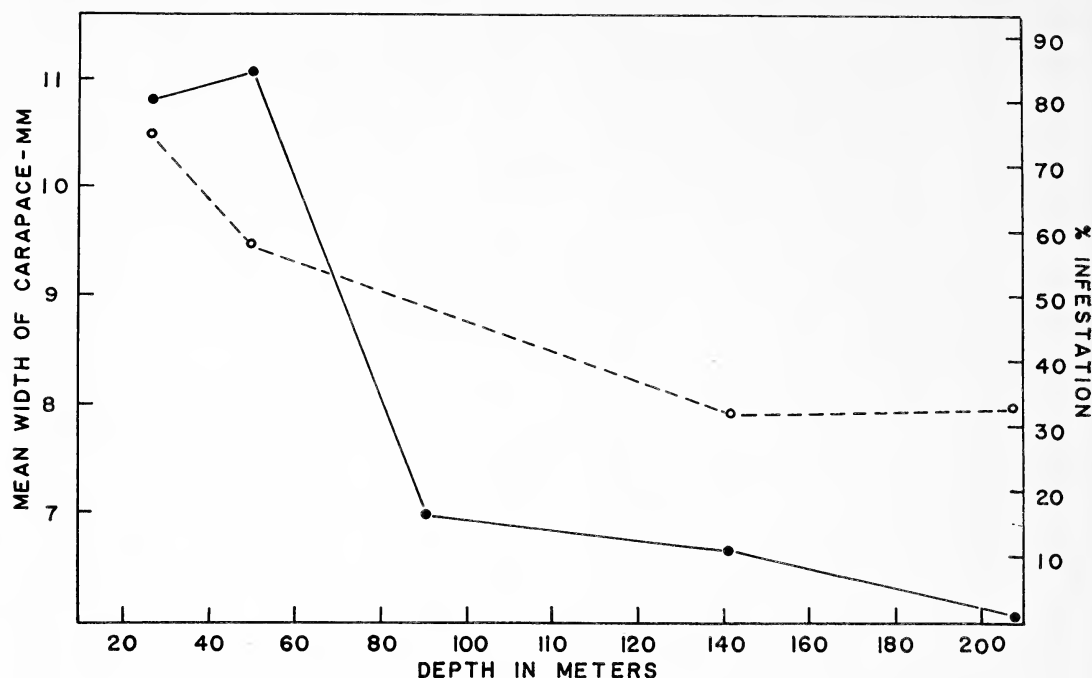


FIG. 1. Curves showing: *dash line*, correlation between mean width of Stage V crabs and depth of water from which their host mussels were collected; *solid line*, correlation between per cent of infestation of host mussels and depth of water from which they were removed.

maturity in relatively shallow waters were, larger on an average, than crabs which have developed and are collected from deeper waters (Fig. 1). This relationship was noted to exist throughout the entire one and one-half years that the crabs were studied. A further discussion of these correlations is deferred to another part of this paper.

The highly colored eggs contained in the gonads show clearly through the thin membranous exoskeleton. The color varies during development; initially appearing chrome yellow, they appear coffee brown immediately prior to their deposition (see Maerz and Paul, plate 9, K-2 and plate 15, A-11). Unless a crab has just become ovigerous, eggs are almost always present in some stage of development. It has been observed that within a week after egg deposition new eggs begin to form and become visible in the gonadal tissues.

While the gonads of Stage IV crabs occasionally contain developing eggs no Stage IV ovigers have been found. It is not until the adult

Stage V instar is reached that egg deposition occurs. The smallest oviger found measured 5 mm in carapace width; the largest was 13.4 mm. The largest crabs collected (i.e., those 14 mm in carapace width), were not ovigerous. However, their gonads did contain large numbers of well developed eggs and it appeared that these were about to be spawned.

The average carapace width of 187 ovigers collected from two depths off Mineral Point (55 and 130 m) was 8.5 mm. These crabs were removed from mussels collected during a period (November, 1959) when the ovigerous females constituted almost 60% of the total population. These ovigers were, on the average, 1 mm less in carapace width than the average of all the Stage V crabs collected during the period of study. This is undoubtedly due to the fact that many of these crabs were still in their first year and had not attained full adult size. In addition, part of this sample was taken, as noted, from relatively deeper waters where the average size of the Stage V is smaller.

Abnormal Instars

Although the sequence of developmental instars, as already described, represents the normal situation, investigations preceding this one have revealed occasional deviations from this general pattern by other pinnotherid species. Orton (1921:533) described a single male *P. pisum* which was morphologically similar to a soft, posthard female. Stauber (1945:280) discussed a second stage, posthard male *P. ostreum* which appeared externally to resemble the Stage II or III females. He notes that they were found in "appreciable" numbers and that their size distribution was somewhat greater than that of the typical Stage I males. He suggested that these atypical males might be "... the result of some sort of parasitism as Mercier and Poisson (1929) have reported for *P. pisum*." Stauber further suggested that these posthard male forms were copulatory partners for the larger posthard females. Christensen and McDermott (1958:152) suggest that the abnormal *P. ostreum* referred to by Stauber were actually prehards and that the greater size range of Stauber's second stage, posthard male over his Stage I series of male crabs was probably due to a sampling error. They do make the reservation that a hard Stage I male may, "now and then," moult to a soft-shelled form. Atkins (1958) presents evidence that, at least in *P. pisum*, the hard or Stage I males do quite frequently undergo a metamorphic moult into a soft posthard form. She has repeatedly observed the same crab change from one form to another with usually two or three soft forms intervening between hard instars. These soft posthard males are usually found during the summer months, June–August inclusive, in southwest England. It is during this period that the males moult and young crabs are found in mussels. Because of this she suggested that the soft posthard males occur during the periods of rapid growth.

A similar situation has been found with regard to *F. subquadrata*. During the summer of 1959 eight Stage I males were observed to moult into soft posthard forms. The latter are similar in body shape to the Stage I instars but are soft and membranous. The pereopods of these soft posthard males are, as those of posthard females,

subcylindrical and with few swimming hairs. Such moults are not accompanied by significant growth. In no case has a posthard male been observed to undergo further moulting, as was observed by Atkins in *P. pisum*.

These posthard male *F. subquadrata* were observed only during the summer months of July and August. This does not necessarily mean that they do not occur at other times, since they could easily have been mistaken for prehard forms had they not been observed moulting from the Stage I instar.

Apparent abnormalities are found not only in the males but also in the morphology of the Stage I females. In these cases Stage I females are noted whose abdomens are precociously widened. This increase in width over that of the normal individuals is quite large, the abdomen–carapace ratio approaching that found in the Stage III females. Other morphological aspects of these individuals tend to be normal, although these forms are invariably larger than the average female Stage I instar. Of 183 Stage I females examined, 5 were of this anomalous type.

Christensen and McDermott (1958:152) report similar anomalies in the Stage I females of *P. ostreum*. In two cases they found individuals considerably larger than the normal Stage I females. Both these crabs had abnormally formed pleopods. However, they do not mention any extraordinary increase in the relative abdomen width of these crabs. It was their opinion that they had been retarded in their development.

ECDYSIS IN *F. subquadrata*

Ecdysis is one of the most significant events in the life history of any crustacean. In a few crustaceans it has evolved to be primarily a mechanism allowing an increase in size to occur. This is true both in the freshwater decapods, the Potamonidae, crabs which hatch from the egg as a replica of the adult (Rathbun, 1918: 11), and in a species of the Oxyrhynca or spider crabs, *Nacioides serpulifera* (Rathbun, 1914: 653). In most marine crustaceans, however, moulting is accompanied not only by increased size but also by considerable morphological change. In no group is this more true than in the family Pinnotheridae. Certainly other

crustacean groups have representatives which undergo extensive changes through ecdysis, but few others, particularly among the brachyuran families, have fitted into the postlarval (post-planktonic) portion of their life cycle such complex morphological changes as accompany ecdysis in the pinnotherids.

While previous investigators have described ecdysis and accompanying phenomena in other brachyurans (Drach, 1939; Hiatt, 1948; Guyselman, 1953; and Knudsen, 1957), little information is available concerning these processes in the Pinnotheridae. For this reason careful notes were made of any moulting activities of *F. subquadrata* during the period of this study. Subsequent studies of ecdysis in *F. subquadrata* as well as other West Coast pinnotherids have been made (Pearce, 1962*b*). These studies involved the use of both light and electron microscopes in determining tissue changes which occur during ecdysis. These data will be included in a separate paper, the present work noting only the macroscopic aspects of ecdysis in *F. subquadrata*.

Two distinct phases of ecdysis can be recognized in all brachyurans. The first is preparatory and, to all outward appearances, is passive in nature although there can be no doubt that physiologically the animal is very active. The second, or active phase, involves the actual exuviation of the cast. This phase is characterized by a great deal of movement by the crab.

Most observations concerning the moulting of *F. subquadrata* were made on animals recently removed from a host mussel. A total of 134 moults were recorded. In 61 of these the dimensions were noted both before and after ecdysis.

Prehard and posthard crabs that are about to moult can be easily detected. One to two days prior to exuviation animals in this state become "creamy" and very opaque in appearance. Unlike other species which have been studied (Hiatt, 1948:155), they do remain quite active. All stages of *Fabia* have moulted under laboratory conditions—some after being held as long as six weeks. Christensen and McDermott (1958:150) found it difficult to obtain moulting *P. ostreum* under the laboratory conditions in which they worked. Unless crabs were "obviously ready to moult on arrival to the laboratory" no moulting occurred in the Petri dishes in which they were

held. These authors, therefore, had to resort to other techniques in order to obtain moulting specimens.

No external change in color or opacity heralds approaching exuviation in the hard Stage I crabs. Only the somewhat more flexible nature of the exoskeleton and the appearance of a crack along the postero-lateral margins of the carapace indicates that ecdysis is under way. The carapace of the Stage I form does not become as soft or decalcified as is indicated for some other brachyuran species (Hiatt, 1948:156); however, a recent paper by Knudsen (1957:134) states that in the California Xanthidae the exoskeleton does not become fragile prior to ecdysis. It may be that, at least in the case of *F. subquadrata*, since the following posthard instars are not heavily calcified the hardening salts remain in the exuviae of the Stage I instar rather than being retained in the crab's tissues to be subsequently redeposited in the new exoskeleton.

About one day after the onset of the opaque appearance in the pre- and posthard crabs a crack appears along the epimeral line, and at this time the active phase begins. The body now expands due to the uptake of water (Drach, 1939; Guyselman, 1953:129). This in effect lifts and frees the posterior portions of the carapace. In the pre- and posthard stages the old integument being shed has the consistency of heavy, wet cellophane. Further, because of its supple nature, it is never lifted to the extent of a 30° angle as was noted in *Pachygrapsus crasipes* by Hiatt (1948:157) or as is found in the Stage I mussel crabs. Rather, the old integument lies free upon the dorsal surface of the new integument of the carapace.

As is noted by Knudsen (1957:136) for the xanthid crabs, it is evident that muscular movements occur during this period since the new integument can be observed to be pulled inward, forming surface depressions.

Following the freeing of the posterior portions of the carapace the last pair of thoracic appendages, the fourth pereopods, and the abdomen are simultaneously freed from the old integument. This is a procedure intermediate between that observed by Knudsen (1957:136), who insists that the abdomen is freed first in

the xanthid crabs which he studied, and Hiatt (1948:157) who reports that in the grapsoid, *P. crassipes*, the legs are first removed, then the abdomen.

As soon as the posterior pair of appendages are free the animal then apparently uses them to exert pressure against the old integument in such a manner as to push the rest of the body free of the exuvia or cast. By this time the crab has moved far enough posteriorly within the cast to allow the more anterior pereopods and mouth parts to be freed. The former can then be pulled into the area vacated by the cephalothorax proper. This description is true of all the pre- and posthard crabs which were observed. In the case of the Stage I crab it is more difficult to determine the manner in which the anterior appendages are freed since the exoskeleton of this stage is completely opaque.

The active phase of exuviation varied between 15 and 45 minutes, with the average time being 20 minutes. The larger crabs (greater than 10 mm in carapace width) took, on an average, somewhat longer. There were exceptions, however. The longest period observed was taken by a Stage III female 5.7 mm in carapace width. There was little difference in the average time required by hard Stage I or pre- and posthard crabs.

In only 2 out of 61 closely observed moultings was *F. subquadrata* seen to moult during the daylight hours. This might seem surprising in view of the fact that mussel crabs are rarely in a photic situation and thus darkness would not be of protective advantage during the crucial period of moulting. However, since most of the freeliving brachyurans do moult at night (Broekhuysen, 1941; McKay, 1942; Hiatt, 1948; and Knudsen, 1957), it can be hypothesized that *F. subquadrata* retains an inherited mechanism involving the inhibition of moulting by light. As noted by these authors such a mechanism would have obvious adaptive advantages to freeliving forms, but it would be of little significance to a symbiotic crab living in a non-photic situation.

The length of time required for the maximum postexuvial expansion to occur was not determined in every observed moult. However, in the cases in which a crab was measured more than

once following ecdysis no measurable expansion was noted after the first postmoult measurement was made. The first postmoult measurement was routinely taken 30 minutes following the completion of exuviation. This implies that the crab expands to its postexuvial dimensions during and immediately following ecdysis, with little or no increase occurring over an extended period following ecdysis. This agrees favorably with the minimum time required for the final expansion of the freeliving xanthid crabs (Knudsen, 1957: 141). The latter required from 30 minutes to 2 hours.

The degree of postexuvial size increment in *F. subquadrata* varies not only with the stage at which the moult occurs but also to some extent between individuals of the same stage. Prehard crabs moulting into new prehard instars had an average increase of 16.5%, with the smaller crabs, i.e., the second or third postplanktonic instars, increasing as much as 20%. Similar increases have been found in the early instars of other brachyuran species (Olmstead and Baumberger, 1923; Broekhuysen, 1941; McKay, 1942; Hiatt, 1948). However, no *F. subquadrata* of any stage ever showed the 400% variation indicated by Hiatt (1948:163) for *P. crassipes*. Generally, during the moulting from the terminal prehard instar into the hard Stage I crab, and from the Stage I into the Stage II instar, there is little or no increase in size.

Only two Stage II females were observed undergoing ecdysis. The first of these crabs showed no increase in carapace width although the abdomen became 20% wider. The other observed Stage II crab increased 10% in carapace width and 40% in abdomen width during the moult into the Stage III form. It is during this moult that a significant change occurs for the first time in the carapace-abdomen width ratio. Needham (1950) has discussed the quantitative aspects of this allometric growth in *P. pisum*.

The moult from the Stage III to the Stage IV instar, in six observed cases, was accompanied by an average 12.2% increase in carapace width and a 65% increase in the width of the abdomen. During this moult occurs the greatest increase in abdomen width relative to the carapace width.

Only a single Stage IV crab was observed undergoing ecdysis. A 10% increase in carapace width occurred during this moult. The abdomen of the new instar (Stage V) increased 34% over that of the original Stage IV crab. Assuming this single observed moult to be typical of all Stage IV crabs, this is a considerable reduction in abdomen increase compared to the Stage III-IV moult. Following this moult (Stage IV-V) the abdomen is, for the first time, either as wide or wider than the carapace, and the definitive adult, Stage V female is attained.

Future ecdysis in the Stage V crabs is largely a matter of increase in size and not an alteration of morphological characters. The average increase in carapace size with each moult of the stage is 9% (in 33 individuals). The abdomen increases an average of 13.1%. It was noted that, as is the case when all stages are considered, the smaller Stage V crabs showed proportionately larger increases than did the larger crabs (greater than 10 mm) of this stage.

The pre- and posthard stages of *F. subquadrata* require only three or four days before an

apparently normal exoskeleton consistency is reached following ecdysis. However, more recent work (Pearce, 1962b) on related species indicates that, while external appearances suggest a "normal" intermoult condition, the actual deposition of new endocuticular lamellae continues for several weeks. The exoskeleton of the hard Stage I crabs requires somewhat longer for the integument to become completely hardened. Three weeks were required by one individual before the carapace was completely calcified and rigid. This could be due to the fact that the animal was kept in an artificial environment in which the normal parameters were not present. Hiatt (1948:163) conclusively demonstrated that changes concomitant with the moulting of *P. crassipes* are affected by prolonged laboratory conditions.

In no case was any self- or exuvial mutilation observed, such as was noted in *P. crassipes* by Hiatt (1948:158) and in the xanthid crabs by Knudsen (1957:140).

Moulting was most frequent during the summer months, particularly during early and

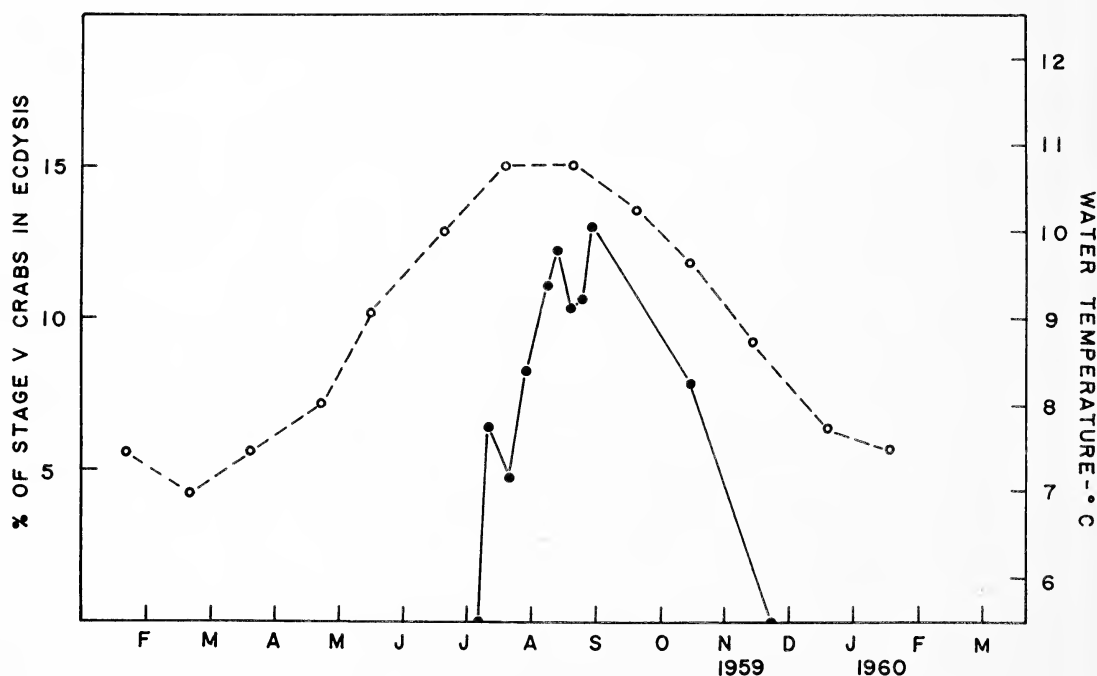


FIG. 2. Curves showing: *dash line*, surface water temperatures taken in the San Juan Archipelago during 1959 and early 1960; *solid line*, per cent of Stage V crabs in ecdysis during the period from February, 1959 to March, 1960.

middle August. During this period as much as 13% of the observed population was undergoing ecdysis. Just as a correlation was noted by Hiatt (1948:161) for *P. crassipes*, so was a correlation noted between monthly temperature means and the percentage of ecdysis for *F. subquadrata* (Fig. 2). The temperatures are surface water recordings made by the U. S. Coast and Geodetic Survey in 1958–59 for the waters of the San Juan Archipelago, and closely approximate the means recorded over a five-year period by Phifer and Thompson (1937). While these temperatures are taken at the surface, it is assumed that they would be valid at the depths from which the mussels were removed since Phifer and Thompson (1937:34) note that the waters of San Juan Channel are very homogeneous to a depth of 100 m.

It was noted that the percentage of Stage V females in ecdysis was greatest during August, regardless of the depth from which they were removed. Figure 2 represents only Stage V crabs and does not include those immature crabs observed undergoing developmental moults throughout the year.

While increased temperature may not in itself be the direct cause for the onset of ecdysis, it may be an indirect factor. Certainly the moulting sequence is correlated in a number of ways with reproduction, the success of which in turn depends upon factors favoring the survival of the zoea. Since it is known that phytoplankton standing crops vary with water temperatures and in turn are important for the development and survival of many zooplankton larval types, including zoea and megalops, so temperature may be correlated with the periodicity of ecdysis.

THE DEVELOPMENTAL CYCLE

Early investigators (Thompson, 1835) assumed that the male pinnotherid sought out his copulatory partner by moving from host to host during the reproductive period. Later Orton (1921:533) tended to substantiate these views by his discovery of individual male *P. pisum* caught between the valves of the host mussel, *Mytilus edulis*. The implication was that the males were trapped while seeking to gain entrance to the host of a female. In addition, Or-

ton found a Stage I female with its spermathecae filled with viable sperm. This latter discovery was repeated by Atkins (1926:478) and was indicative of a precocious copulation in *P. pisum*.

Examination of mid-water plankton trawls made by members of the Department of Oceanography of the University of Washington in the southern waters of Puget Sound during May, 1957 resulted in the finding of 56 Stage I *F. subquadrata* of both sexes. Examination of materials collected in a similar manner prior to and subsequent to this period revealed a paucity of these crabs, only 2 being found. Microscopic examination of the spermathecae of the females taken in the trawls, as well as those removed from host mussels, revealed that *F. subquadrata*, like *P. pisum* and *P. ostreum* (Christensen and McDermott, 1958), copulates precociously.

Since the sample taken from these plankton tows represents the only time that female and male *F. subquadrata* have been found together, it is probable that copulation in this species occurs during a period when both the male and female Stage I crabs leave their host bivalves and assume a temporary freeliving existence.² Of the total of 56 Stage I *F. subquadrata* taken in these tows, 29 were males and 27 females. Conversely, in only 3 out of 2,088 total observed infestations were double infestations of the host mussel ever found. In 2 of these cases 2 male Stage I crabs were found together, and in the remaining example a Stage I female was found together with an unsexable prehard crab.

If copulation occurs while the female is in the Stage I form, as seems likely from present evi-

² It has only recently come to my attention that Sakai (1939:604) has reported a similar swarming in the pinnotherid, *Tritodynamia borvathi*, which is found in Japanese and Korean waters. He notes that both males and females swarm together in large numbers. The swarming or migrations occur in Japanese waters "... from the middle of autumn to the beginning of winter." In Tinkai Bay, Korea, however, Kamita (1935:36) reports it as occurring in June and July. The crabs are often found in such dense numbers that they are harvested and used for fertilizer. In addition, large schools of fish follow the moving crabs, obviously feeding upon them. No ecological significance was attached to the swarming, and Sakai does not distinguish at what stage of the life cycle the swarming occurs.

dence, and if copulation were consummated in the host mussel, it would be expected that occasional pairs of males and females would be found in the large numbers of mussels examined throughout the year. Such double infestations have not been found, however. Furthermore, the finding that Stage I males and females swarm together in open water gives evidence that the copulatory act takes place outside the host. This is contrary to what other investigators have found to be true in related pinnotherids (Thompson, 1835; Orton, 1921:533; and Christensen and McDermott, 1958:166).

More recent evidence, involving the attraction of swimming Stage I crabs to a "night light" used at the Friday Harbor Laboratories, indicates that the swarming behavior is probably restricted to late May and early July. Of eight crabs taken in this manner during the spring and summer of 1961 only one was obtained later than mid-June and none earlier than the 4th of May.

It is of interest that the average sizes of the swarming Stage I males and females, taken in the mid-water trawl and at the "night light," are approximately the same. The average carapace width of 32 males is 3.51 mm, while the same number of females averaged 3.58 mm.

Collection data show that swarming was not restricted to only one station or limited area. Rather, it was found to occur at several widely separated stations in the San Juan Archipelago and Puget Sound. Since the host mussel is widely distributed in these waters, it would be expected that the crab symbiont is found equally dispersed.

A current investigation of *Pinnotheres maculatus* as part of the benthic community in the Woods Hole area indicates that this species also engages in a copulatory swarming. In 1963 this swarming reached its peak during the last two weeks of October. A more detailed account of this and other aspects of the biology of *P. maculatus* will appear in a later paper.

When all the material collected from the San Juan Archipelago area in 1958-59 is considered, it is clear that the greatest number of ovigerous females appears during the winter months. Large numbers are initially found in early November and form a significant portion of the population

through the middle of February, with a peak at the last of January. As many as 75 (60%) of the total adult population of 126 Stage V females collected off Point Caution on January 28, 1959 were ovigerous. Collections made during the winter of 1959-60 indicate that the ovigers were more numerous earlier in the season during this particular year. A sample of 22 Stage V crabs collected off Mineral Point and examined on November 23, 1959 contained 19 ovigerous crabs (87%). Large percentages of ovigers were found at the other collecting sites during this period.

Since the swarming females copulate in late May, an interval of some 21 to 26 weeks would ensue before the start of egg deposition in November and December. During this period the precociously inseminated female must undergo the series of growth and metamorphic moults which have already been described. Because there is no overwintering of immatures as reported for *P. ostreum* by Christensen and McDermott (1958:158), the number of immatures, both male and female, present in the population is low during the winter months of November, December, and January.

The immature crabs are found in greatest numbers during the early- and mid-summer months. On July 21, 1959 they constituted 56% of a total sample of 119 crabs collected off Point Caution. They formed a comparable percentage of the population at the other stations during the period of June 15-August 1. The Stage I crabs were particularly prevalent in the samples taken during May. The collection taken at Mineral Point on May 4, 1959 included 37 Stage I instars. These 37 crabs constituted 31% of the total population. The remainder were mostly prehard stages which would moult into the Stage I form before the month was over. The early posthard forms (the Stage II and III instars) were more in evidence during June and early July, with the later posthard forms (the Stage IV and V instars) becoming prevalent in August and September.

From the discussion above and Figure 3 it is obvious that the ovigerous females occur predominantly during the months of November, December, and January. During February the eggs begin to hatch and the new larvae spend

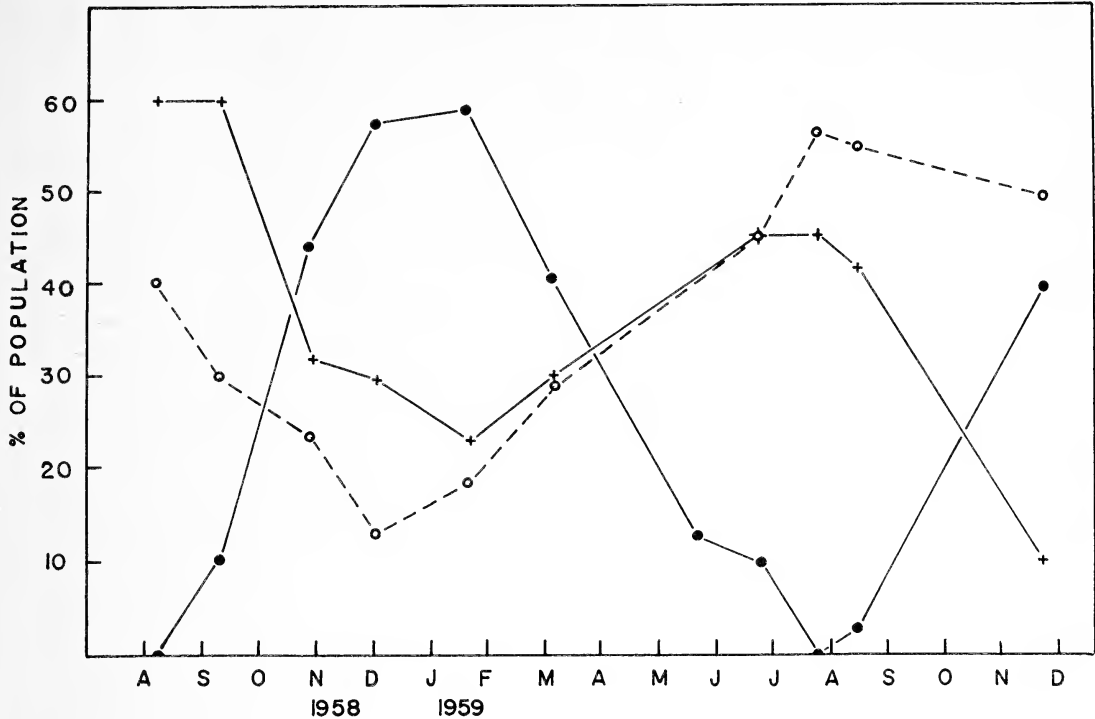


FIG. 3. Curves showing per cent of total crab population constituted by: solid line broken by circles, ovigerous Stage V females; solid line broken by crosses, nonovigerous Stage V females; dash line broken by circles. immature crabs of both sexes. Samples collected from San Juan Channel off Point Caution, San Juan Island. Washington between August 8, 1958 and November 23, 1959.

upwards of eight weeks in attaining the first true crab stage. Hart (personal correspondence) has recently reared *F. subquadrata*. She found that eggs laid on October 27, 1958 hatched on February 6, 1959 and moulted into the first true crab stage on April 6, 1959. As already discussed, it is assumed that the first crab stage enters an initial bivalve host, usually *Modiolus modiolus*, and completes a series of prehard moults which culminate in the hard, Stage I instar. This is true both of the male and of the female. It is suspected that in general the prehard series occupies the interval between early April and late May. At this time the Stage I crabs leave their hosts and engage in the swarming activities which culminate with copulation. Following these activities the Stage I female, and at least some males (since larger Stage I males occur in the collections throughout the remainder of the year), return to a bivalve host, where the female undergoes a series of at least four posthard

moult which terminate in the definitive adult, the Stage V crab.

The immature posthard and Stage V crabs retain the full spermathecae which result from the precocious copulation of the Stage I instar. Non-ovigerous Stage V females are present in the greatest numbers during August, September, and October, and this is the period when the numbers of immature crabs are sharply decreasing. During late October and early November the ovigerous females become more numerous and once again, during mid-winter, they constitute the majority of the population.

There is a period of three months between the time the Stage V crabs are first found in increasing numbers and when the ovigerous females are noted to represent a significant portion of the population. Furthermore, since many Stage V crabs are found moulting during this period one may assume that at least one or two moults will occur in this period. This assump-

tion is supported by the fact that the earlier Stage V crabs (found in late summer) are always smaller on an average than are the ovigers taken later in the year at the same station and depth.

The only previous study concerning the complete postplanktonic life cycle of a pinnotherid is that made by Christensen and McDermott (1958). They found that: (1) the number of Stage I *P. ostreum* was at a minimum during the winter and spring months and that in June large numbers of Stage I crabs appear in the oyster hosts; (2) the Stage I crabs represented, during this period, up to 60% of the total population; (3) 45% of the Stage I crabs were males; (4) by the end of July only 5% of the crabs collected were males and by early September not a single male could be found.

In addition to the ultimate disappearance of the males from the *P. ostreum* population they noted that during a period in late June a significant number of double infestations began to appear. They suggested that these could only be due to new invasions by male Stage I crabs seeking copulatory partners within the host oyster. In view of this fact, and of the present observations that *F. subquadrata* engages in swarming and the male survives through the summer, it can only be assumed that *P. ostreum* and *F. subquadrata* have diverged widely in their reproductive habits.

It is believed that some female *F. subquadrata* live for more than one year and also reproduce more than once. Figure 3 shows that there are always residuals of the nondominant stages. For instance, in the summer when the immature instars (of all stages) predominate, there is always a percentage of Stage V crabs and occasionally an ovigerous female. Since these crabs were frequently much larger than average (often greater than 12 mm in carapace width) it is thought that they are remnants of the previous year's adult population and not merely precociously developed individuals of the present year. Christensen and McDermott (1958:159) present evidence that *P. ostreum* may live as long as three years. There can be no doubt, however, that some of the smaller, "residual," Stage V *F. subquadrata* are the result of spawnings occurring somewhat earlier in the year than the majority

It is possible that they are the offspring of second year females.

The immature crabs which are found later in the season and throughout the winter (Fig. 3), when the Stage V crabs are predominant, are almost certainly the result of the egg deposition subsequent to the period when the majority of the crabs spawn. Similarly, Stage I males are found throughout the winter. Since they too are larger than the average Stage I males collected during May, when the swarming occurs, it is believed that they represent a remnant of the male population of the previous summer.

Atkins (1955:689) has shown that it is possible for one implantation of sperm to successfully fertilize a second egg deposition which might be produced by a female *P. pisum*. Christensen and McDermott (1958:167) also present evidence tending to confirm the same thing in *P. ostreum*, as do Wells and Wells (1961:275) in *Pinna xodes floridensis*, and Pearce (1962*b*) in *Pinnixa faba* and *P. littoralis*.

Whether it is possible for a second copulation to occur in *F. subquadrata* is extremely doubtful. Christensen and McDermott (1958:167) report what might be a copulation between a male, Stage I crab and a female, Stage V instar of *P. ostreum*. They doubt, however, that such a copulation would normally occur in this species. If copulation in *F. subquadrata* is restricted to the period of swarming in open waters it is obvious that, because of its morphology, the Stage V instar can never leave the host and is thus unable to copulate a second time in open water. Since no Stage V female has ever been noted to be accompanied by a hard stage male or, for that matter, a male of any other stage, it can probably be assumed that a second infestation is not tolerated and it is thus doubtful that a second copulation would or could occur. Furthermore, as was pointed out by Stauber (1945:270) for *P. ostreum*, the size difference between the average adult female and the hard stage male probably makes copulation mechanically impossible.

GROWTH AND DEVELOPMENT CORRELATED WITH HOST SIZE

Wells (1940:45) found that a definite positive correlation could be established between the

carapace width of the mussel crabs and the length of their host mussels: by grouping shell lengths and plotting them against the mean carapace width of all the crabs found in each shell length group, he could obtain a curve indicating that the carapace width was, in general, proportional to the shell length of the host. Atkins (1926:482) was able to find a size correlation between 34 *P. pisum* and their bivalve hosts. More recently Christensen and McDermott (1958:160) established a similar relationship between all stages of *P. ostreum*, as well as for only the Stage V instars of that species, and their host, the American oyster, *Crassostrea virginica*. The latter proposed that external factors, with the amount of food probably being the most important, act upon both the bivalve and its symbiont crab so as to regulate the growth of the crab in such a manner that it "fits" the host.

They further note that while smaller crabs may occasionally be found in proportionately larger bivalves, the converse seldom occurs, i.e., large crabs are rarely found in proportionately smaller oysters.

The present work extends that of Wells, who used a relatively small sample of 111 unstaged crabs in his study. During the present investigation examination of 305 crab-mussel associations has resulted in the curve presented as Figure 4. This curve, derived from material collected at one station during the period July 8 to November 11, 1959, is indicative of this correlation.

After examination of the host mussels for the presence of the pinnotherid crabs two rather interesting facts emerge. One was that immature crabs are almost always found in the proportionately smaller host mussels. This is true even

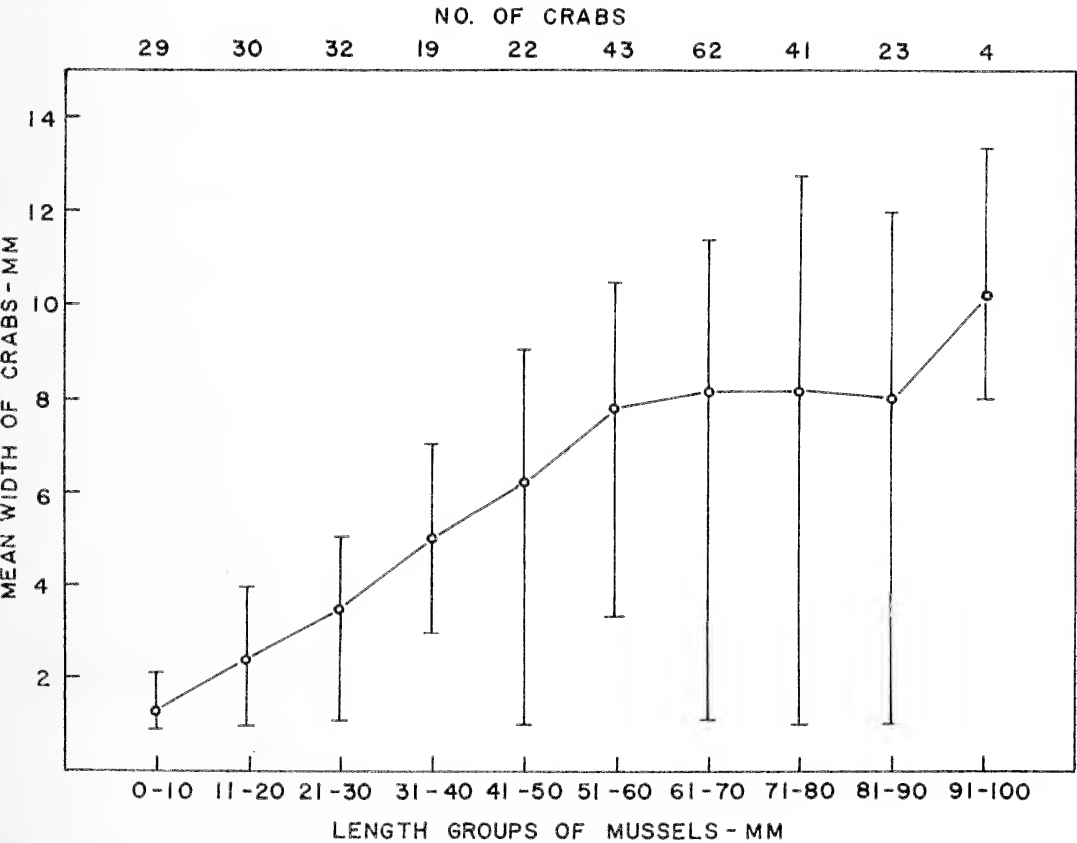


FIG. 4. Curve showing positive correlation between carapace width of all stages of *F. subquadrata* and length of host mussels from which they were removed. Both mean width and size range are given for the crabs.

though the larger mussels could obviously accommodate them. Second, the very large mussels, i.e., over 85 mm in length, seldom contain a crab. It is easy to see, as did Christensen and McDermott (1958:161), why small mussels only rarely contain relatively larger crabs. The reverse, however, is not so easy to explain, i.e., why are smaller crabs seldom found in relatively larger mussels? Also, why is it rare that few crabs, of any size, are found in the very large mussels above 85 mm in length, the latter in spite of the fact that such mussels are relatively abundant?

The occurrence of the early postplanktonic stages has been noted only in the mantle cavity, and not throughout the entire water-conducting system as noted for *P. ostreum* by Christensen and McDermott (1958:173). Therefore, it is not felt that such crabs have been overlooked in the microscopic examination of the larger host bivalves.

Because the very small prehards and invasive stages (1.0 mm or less in carapace width) are most frequently found in the smaller mussels (15 mm or less in shell length), it is thought that the newly moulted true first crab stage, when settling out of the plankton, usually selects a mussel of this size for its host. Figure 5 indicates that 80% of the true first stage crabs are found in mussels ranging from spat to 20 mm in valve length. The mechanism affecting this selection is not definitely known, but at least two possibilities might be suggested.

It is possible that the smaller mussels use qualitatively or quantitatively different food materials than do the larger mussels. Further, it is quite possible that the invasive and other prehard instars require a similar size or type food and are thus obliged to infest initially the smaller, immature mussels. Small crabs which fortuitously find their way into compatible small mussels would survive, while those crabs that infest the larger mussels would not. The fact that occasionally small, invasive stage crabs are found in larger mussels (Fig. 5) could be explained by regarding these crabs as in a transient situation, in which the mussels have only recently become infested by the invasive crab, which would soon be eliminated. The waste which would accompany this elimination is another example of the normal larval or juvenile

"wastage" noted by Thorson (1950:3) in so many marine forms.

The second suggestion involves the hypothesis that the crabs are attracted, selectively, to the smaller mussels by a "host factor." Recent studies by Davenport (1950, 1953a, b), Johnson (1952), Hickok and Davenport (1957), and Sastry and Menzel (1962) indicate that in certain cases of symbiosis the commensal or parasite is indeed attracted to the host by a diffusible factor from the host. The same factor may be used to maintain the relationship once it has been established. Preliminary work recently carried out by Davenport (personal communication) at the Friday Harbor Laboratories did not reveal evidence to support the existence of any such mechanism between *F. subquadrata* and its host, *M. modiolus*. It is important to note, however, that these experiments were conducted only with the Stage I and older instars; and it is quite possible, in fact probable, that such an interaction might be found only between the invasive stage and its host, and perhaps even at a particular time during the instar's existence.

Johnson (1952) reported that a chemotaxis existed between the pinnotherid, *Dissodactylus mellittae*, and the echinoid, *Mellita*. His work with two other pinnotherid species, however, did not reveal the existence of any attractive mechanism between them and their hosts. He suggested that the chemotaxis between *Dissodactylus* and *Mellita* acted to enable the pinnotherid to maintain a continuous relationship with the host in an environment (heavy surf) in which they might readily become separated. In the *Pinnixa chaetoptera*-*Chaetopterus* relationship, as well as the *Pinnotheres*-*Ostrea* relationship, both of which he studied, it was suggested that the negative evidence for the existence of a host factor might be the result of using the experimental devices with a stage of the crab's life cycle which is not attracted to the host. It might well be that other stages do respond.

The recent study by Sastry and Menzel (1962), while indicating that *Pinnotheres maculatus* is attracted both to the bay scallop, *Aequipecten irradians concentricus*, and the penshell, *Atrina rigida*, makes no mention of the stage of the females used in the experiments. They do

distinguish between adult and "early" male stages, although this distinction is not evident in the summary of their experimental results.

The hypothesis that the invasive stage *F. subquadrata* is selectively attracted to the immature spat of the host mussel is made more plausible in the light of recent evidence presented by Blake (1960). He has found that the predator oyster drill, *Urosalpinx*, is attracted selectively to its prey, *Crassostrea virginica* and *Modiolus*

demissus, on the basis of oxygen consumption (used as an index of metabolic activity). One of four factors affecting the metabolic rate was the age of the prey (the others were species, growth rate, and feeding). Both Haskin (1950) and Carriker (1955:49) have shown that there is a predilection by the drills in their choice of younger prey. It is hoped that further investigation of this aspect of the relationship between *F. subquadrata* and *M. modiolus* can be made in

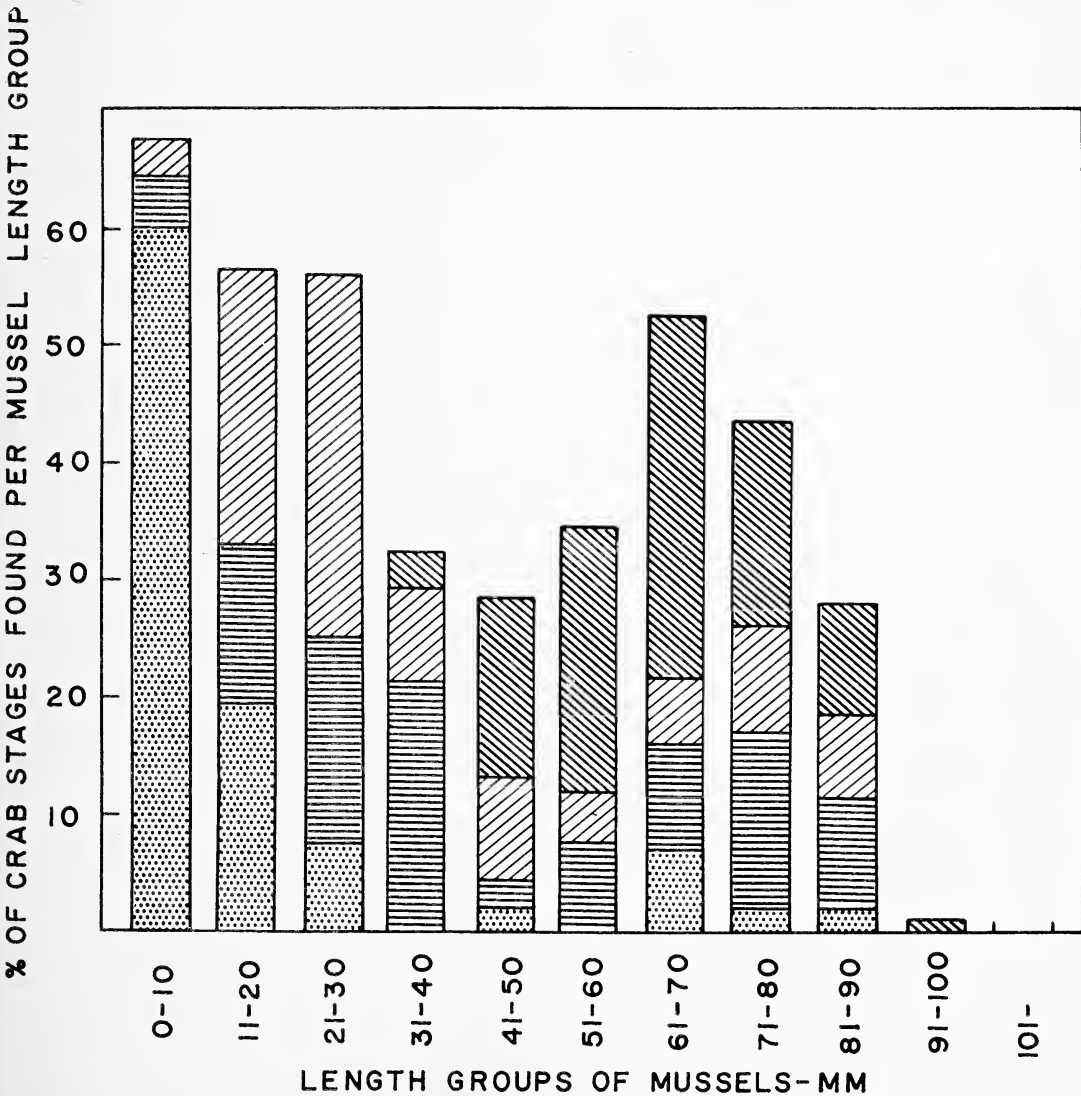


FIG. 5. Histogram showing percent of first true crab stage (stippled fraction of bars), immature females of all stages (horizontal lines), males (fine oblique lines), and Stage V females (heavy oblique lines) found in each length group of the host mussel, *M. modiolus*.

order to attempt to establish the validity of the hypothesis that the invasive stage crab is attracted to the smaller host mussels on the basis of the latter's relatively higher metabolic rate.

An experiment, in which first stage crabs or very early prehardes were placed in small, previously uninfested mussels, indicates that the growth rate of these mussels was sufficient to accommodate the growing crabs. More details regarding this experiment will be presented in a separate paper.

While the foregoing discussion suggests some reasons for the propensity of smaller crabs to associate with the proportionately smaller mussels it does not give any indication regarding the almost general absence of crabs from the

very large mussels over 85 mm in length. It has been reported that *M. modiolus* is an extremely slow grower in its later years and quite long lived (Wiborg, 1946; Coe, 1948). Wiborg reports that off the coast of Norway the horse mussel attains its maximum size of 118 mm at an age of 18 years. It is therefore quite possible that the hosts outlive their original symbiont crabs. Furthermore, since there appears to be a tendency toward the initial infestation of the small, immature bivalves, these larger host mussels might never be reinfested once their original symbiont crab has perished. This would be especially true if the host mussel is selected by the invasive crab on the basis of relative metabolic activity.

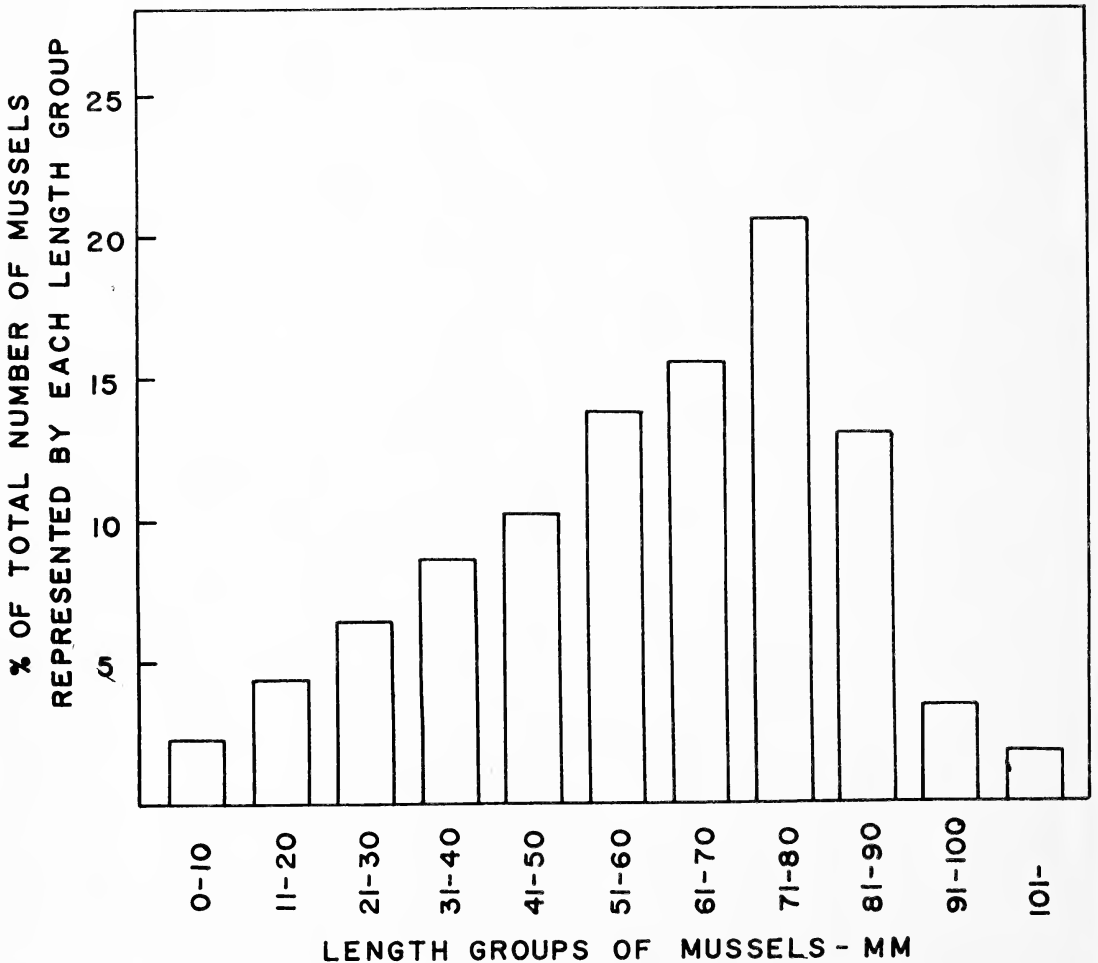


FIG. 6. Histogram showing per cent of total population of *M. modiolus* constituted by each length group.

Observations on the percentage of infestation of the various size groups in the mussel population tend to confirm this speculation. From Figure 4 it may be seen that the average adult size (8 mm) of the crabs on this date is reached in the mussel length group of 51–60 mm. This same average size is also typical of the crabs found in the larger mussel length groups, i.e., larger than 60 mm, although the total number of adult crabs found in each mussel length group decreases above the 61–70 mm range (Fig. 5). This decrease in the number of crabs per group is probably due to the postreproductive mortality following the adult and ovigerous stages. It can also be noted that the greatest number of mussels is found in the 71–80 mm length group (Fig. 6); and furthermore, while there are almost as many mussels to be found in the 81–90 mm group as in the 61–70 mm range, the number of infested mussels in the former group is only one-third that in the latter. Since this is generally true of the mussel populations at all the collecting sites, it seems to indicate that the crabs are outlived by their hosts which, usually, are not subsequently reinfested.

Closely related to the problem of the size relationship existing between *F. subquadrata* and its host is the problem of how permanent is the relationship between the crab and its individual host mussel once this has been established. Does the crab remain within the host after having initially infested it, or is the relationship transitory, with the crab at some period leaving the host?

Rathbun (1918:62), Orton (1921:533), and Berner (1952:345) all suggested that the various hard stage male pinnotherids with which they worked were freeliving. Christensen and McDermott (1958:175) doubt this for *P. ostreum* and *P. pisum*, and they report that the male leaves the host only temporarily during the copulatory period to seek a mate. They state also that this migration is only a phase in the ordinarily commensal or parasitic life of the crab. More recently, Sastry and Menzel (1962:390), in their discussion of the chemotactic responses of the pinnotherid, *Pinnotheres maculatus*, to its bivalve hosts, quote Rathbun (1918:76) to the effect that the early stages of the male are freeliving whereas the later adult males

are commensal in habit. A current investigation of this species in the temperate waters off Cape Cod indicates that, as with *P. ostreum* and *F. subquadrata*, all the stages, with the exception of the invasive first true crab stage and the swarming Stage I instar, are normally symbiotic.

It has been observed that Stage V crabs and posthard forms can and do vacate a host mussel which is moribund. This is, however, the only time that these stages have been found outside a host organism under laboratory conditions.

During August 1959 several immature crabs were found in bivalves not previously recorded as hosts for *F. subquadrata*. The new host species include *Astarte compacta*, *Cardita ventricosa*, *Crenella columbiana*, and *Kellia* sp. All these species are quite small. None, according to Oldroyd (1928), reaches a length greater than 25 mm. One of them, *C. columbiana*, rarely exceeds 16 mm. All the crabs found in these hosts were either prehard or Stage I crabs. Because none of these bivalves normally attains a size sufficient to contain an adult *F. subquadrata* it is thought that the Stage I crabs, after leaving these small initial host species to take part in the copulatory swarming, do not return to the smaller bivalve species but rather secondarily infest a larger host, usually *M. modiolus*. If the smaller initial host species are reinfested by postswarming crabs it is quite likely that the definitive adult crab stage is not attained. Examination of 262 individuals of these small bivalve species has not revealed the presence of a single adult crab.

A comparable host change has been described for *P. pisum* by Christensen (1958:3). He found that on the west coast of Sweden the first crab stage initially infests the lamellibranch *Spisula solida* and that later, upon reaching the Stage I instar, it leaves *S. solida* and secondarily infests *M. modiolus*. The major difference between *F. subquadrata* and *P. pisum*, in this regard, is that in the latter the host change between lamellibranch species seems to be regular or obligate, whereas *F. subquadrata* appears only occasionally to undergo interspecific change, the usual situation being intraspecific. In a more recent report, Christensen (1962:6) notes the occurrence of an ovigerous *P. pisum* in a primary host, *S. solida*, collected at Frederikshavn, Denmark, in the summer of 1960. This indicates

that *P. pisum* is occasionally capable of reaching adulthood in the primary host.

THE RELATIONSHIP BETWEEN *F. subquadrata* AND ITS HOST, *M. modiolus*

By placing various stages of *F. subquadrata* within mussels which have had a "window" opened in one of the valves, in the manner reported by Orton (1921) and MacGinitie and MacGinitie (1949:313), it has been possible to observe the behavior of the crabs within the host.

Probably the most noticeable feature of the relationship is the comparative inactivity of the Stage V crab within the bivalve host. Most of the movements noted were associated with feeding activities.

The adult female, without exception, is found occupying the anterior half of the mussel's mantle cavity. This is generally the widest part of the mussel. The crab's abdomen is always placed against a pair of demibranchs, with the carapace facing the center of the mantle cavity and the frontal region oriented ventrally with respect to the mussel. Such a position insures that the chela and mouth parts of the crab are in a position which facilitates feeding. The crab maintains this position by inserting the dactyls of the pereopods into the gill filaments and/or mantle tissues.

In general the feeding is, as described by Orton (1921) for *P. pisum*, a matter of picking the mucous food strings from the food grooves of the ctenidium upon which the crab is sitting. The chelae are used initially to catch the strings which are passed to the mouth parts. The anterior pair of pereopods are observed sometimes to play a part in the manipulation of the food strings.

Prolonged feeding in this manner ultimately results in extensive ctenidial erosion, as was reported as occurring in *Crassostrea virginica* (Stauber, 1945:284) and *Mytilus edulis* (McDermott, 1962a:163) due to the presence of *P. ostreum*. Ctenidial or gill erosion caused by adult crabs involves the entire portion of the ctenidium underlying the crab. This portion of the gill is eventually destroyed. Figure 7 reveals this damage and shows the difference between

the eroded and undamaged ctenidia of a mussel. The damage seems to be caused by the constant contact of the chela against the edge of the ctenidium. It is also noted that the crab "nips" at the food string with the chela, and very likely the gill margins will also be pinched and cut as a result of this action. Damage to the palps often accompanies ctenidial erosion, and they may be much reduced in length as well as malformed due to the presence of a pinnotherid crab.

Besides the effects of the chelae during feeding, the dactyls of the pereopods, used to support the crab, also contribute to the gill erosions. By repeatedly inserting the dactyls into the gill lamellae the crab causes progressive erosion dorsally from the point of the initial damage. Once the entire underlying gill has been eroded away the crab maintains its position by inserting the dactyls into the mantle. This results in a pathological condition in which the constant irritation by the dactyls causes a blister or cyst-like formation. This anomaly was found to be present in 55% of the mussels infested with Stage V crabs. A similar condition has also been reported in *Anomia simplex* infested by *Pinnotheres* (McDermott, 1962a:163). As the erosion progresses dorsally toward the suspension of the ctenidium, the food groove is continually reconstituted. Without such a continuous regeneration it is doubtful whether the crab-mussel relationship could long endure, since the food groove is necessary to the feeding process of both organisms. Atkins (1931) has reported a similar regeneration of the food groove following deliberate mechanical damage to the gills of *Mytilus edulis*.

As reported by Stauber (1945:284) for *P. ostreum*, the ctenidial damage inflicted by the immature *F. subquadrata*, especially the Stage I forms, differs markedly from that described for the adult crabs. Because the Stage I crab is considerably smaller, and much flatter dorso-ventrally, than the Stage V crab, it is able to move about more extensively within the confines of the host. As a result of this movement the gill erosion is not restricted to the area beneath and in immediate contact with the crab, but is found along the entire margin of the ctenidium. Moreover, erosion of both ctenidia is common. These erosions quite often cause the



FIG. 7. Photograph showing damage done to ctenidia of *M. modiolus* by a Stage V crab 9.3 mm in carapace width. Note that the ctenidia lying in the left (*lower*) valve are eroded dorsally to the line of suspension. The ctenidia in the right (*upper*) valve are almost entire and serve for comparison. Cystlike anomalies can also be noted on the mantle tissues of the left valve. $\frac{1}{3} \times$.

gill edges to appear serrated. Indentations caused by immature *F. subquadrata* are only one-fourth to one-third the dorso-ventral dimension of the gill, whereas the gill damage caused by the adult crab almost always appears as a single, crescent-shaped erosion, often extending to the base of the ctenidium (Fig. 7).

It appears likely that the erosion of a mussel's ctenidia always starts with the small-crab type and, as the crab matures, the damage becomes that typical of infestations with the adult crabs. Christensen and McDermott (1958:171) note that the erosion caused by *P. ostreum* in the American oyster also progresses from an initial small-crab type damage to the more extensive destruction of tissues connected with the

infestation by a large adult crab.

It is noteworthy that only 58% of the small-crab infestations seen during the months of June and early July are accompanied by extensive erosion, while Stage I infestations prior to and following this period are almost invariably accompanied by extensive, small-crab type erosions. This effect could quite possibly be due to the infestation of previously uninfested mussels following copulatory swarming by the crabs, which thus did not have time to cause extensive erosion.

Both kinds of damage appear to be about equally detrimental to the individual host mussel. Because the smaller Stage I or prehard crabs are usually associated with smaller mussels, the

small-crab type erosion is prevalent in hosts of this size range. Similarly, while the small-crab type of erosion may not appear to be as extensive as the adult-crab type, it may well result in as much, or more, relative surface area being removed from the ctenidia. In addition, the food groove in the former type of erosion may be mutilated over much of its entire length, and it is this structure which is essential to the feeding of the host mussel as well as the symbiont crab. Finally, small-crab damage, unlike adult-type erosions, usually affects both ctenidia.

It is apparent from the foregoing that *F. subquadrata* is not the harmless commensal that it has been considered to be (Wells, 1940:26; MacGinitie and MacGinitie, 1949:312). As does *P. ostreum* this pinnotherid induces an actual physical damage to the mussel host which by its very nature must be harmful to some degree. Under normal conditions, however, the crab is a very effective parasite. Its presence does not seem to affect the growth of or cause the death of the host, nor does it appear to so weaken the host as to render its own position precarious. However, under other than normal conditions the effect of the relationship may be more serious. As Hopkins (1957:414) points out, "... an organism which robs its host of nourishment must be harmful in some degree, even if the host shows no apparent effect, but under favorable conditions it is probably not difficult for the host to compensate or even over-compensate for the loss by ingesting more food. Under conditions of food scarcity the same parasite might become harmful."

That such a situation may possibly occur can be shown by studies of the distribution of the crab with regard to water depth. Mussels removed from relatively shallow waters, i.e., 20–60 m, have a much higher percentage of infestation than do mussels taken from waters at a depth of 200 m. Mussels collected from waters of intermediate depths (120–140 m) have a percentage of infestation intermediate between those typical of shallower and of deeper waters. As seen in Figure 1, mussels removed from 30–60 m of water are consistently more than 80% infested. Mussels removed from waters 200 m and greater in depth are rarely more than 2% infested and frequently less than 1%.

Within the waters surrounding the San Juan Archipelago this relationship of the degree of infestation to the water depth appears to hold regardless of the geographic area from which the mussels are removed. Mussels from the shallow waters off Point Caution, San Juan Island, have more than an 80% infestation just as do mussels removed from the shallow waters off Point Lawrence on Orcas Island, and Pea Vine Pass, all relatively separated areas. Mussels removed from any of the deeper waters of President Channel always have a low percentage of infestation.

It was also found that the mussels themselves removed from the deep waters of President Channel were in very poor condition. The gonads usually appeared atrophied, while the visceral masses were, in general, very much reduced. The valves of these mussels, while on the average the same approximate length as those from shallower waters, were thin, brittle, and much more subject to breakage than were those of the shallow water mussels.

Wright (1917) reports that *Pinnotheres* never, or at the most very rarely, occurs in poorly nourished mussels, although it was frequent in those forms from areas where the host mussels were obviously well nourished and making rapid growth.

Thus it can be concluded that when host mussels occur in an environment that is deficient in some factor the infestation by the pinnotherid crabs is reduced, either primarily or secondarily, by the same limiting factor. On the basis of known information it cannot be determined what the limiting factor might be in the present case. Considering the poor physical condition of the mussels found there, it is possible that there may be a deficiency in the amount or kind of available nutrients in the deeper waters.

A number of recent papers (Blake, 1960; Haskin, 1940, 1950; Janowitz, 1956) have indicated that certain gastropod predators are able to locate their prey on the basis of the latter's relative metabolism. Apparently the diffusible end products of the metabolic processes of the host species form gradients up which the predator is able to move. Similarly, Wilson (1948) has recently demonstrated the ability of certain larval forms to "select" appropriate substrates

upon which to settle. Therefore, it does not seem improbable that the settling first stage crabs and the postswarming Stage I crabs might use similar metabolic "targets" in selecting their hosts. This not only would account for the lack of infestation in the poorly nourished, and hence slower metabolizing, mussels found in the deeper waters, but also could explain, as previously discussed, the propensity to infestation of smaller, and probably more rapidly metabolizing, mussels by the early postplanktonic first crab stages.

Finally, the author does not discount the fact that the hazards encountered by these crabs, in settling in deeper water, are much greater and that hence the low levels of infestation found in such conditions may only reflect the loss incurred during the extended settling period.

Houghton (1963:257) reports that there is a correlation between the incidence of infestation of *Mytilus edulis* by *P. pisum* and the tidal level at which the host mussels were collected. He suggests that this is because the first true crab stage of this species is photonegative, and hence it is not likely that mussels found on the shore or at the surface on floats will be invaded.

One further testimony to the delicate balance of this relationship is the fact that double infestations occur only very rarely. As reported elsewhere in this paper only three such cases were noted in this study. This is dramatically different from the condition reported by Stauber (1945:281) and Christensen and McDermott (1958:155), who found that multiple infestations by immature *P. ostreum*, even of spat, were very common during certain periods of the life cycle. However, they did not ever observe two posthard crabs occurring in the same host. Using the same survey techniques as those employed during my investigation of *F. subquadrata*, they recently observed that frequently a single, adult *Mytilus edulis* is infested with up to six prehard *P. maculatus* as well as with an adult female. In this respect, then, the behavior of *F. subquadrata* differs markedly from that of both *P. ostreum* and *P. maculatus*.

The strong tendency toward single infestation observed in the case of *F. subquadrata* certainly suggests some mechanism which selects against multiple infestation of a host organism that is

unable to accommodate the activities of more than one pinnotherid. It appears obvious that, in the case of the *F. subquadrata*-*M. modiolus* relationship, an infestation by two adult crabs would reduce the food gathering surface of the ctenidia to a level below the minimum required to sustain three organisms. Since double infestations are not ever observed between the host and two immature crabs, it would appear that the supposed mechanism operates below the adult level, i.e., at the first stage and/or Stage I levels.

As noted by Wells (1940:34), Stage V females display a marked hostility toward each other when placed together in finger bowls. However, the present investigation has revealed that immature forms (even Stage IV instars), similarly situated, do not demonstrate the marked aggressive behavior which characterizes the adults' relationships. It is notable, however, that when two Stage I crabs are placed in a mussel one, and sometimes both, will immediately vacate the host. This was true in six replicate trials. On the other hand, when a single crab is inserted it will remain within the host.

The relationships between the mussel crab and the alternative, smaller species of bivalve hosts already mentioned are not known as yet. A cursory examination of these hosts did not reveal extensive damage to gills or other parts. The infesting crabs were mostly immature prehard crabs (94 out of 120 such infestations, or 78%), and extensive damage probably would not have had time to occur.

F. subquadrata has also been recorded as occurring in *Mytilus edulis* (Wells, 1928:289), *M. californianus* (Wells, 1928:289; Ricketts and Calvin, 1952:164), and *Saxidomus* sp. (Hart, personal correspondence). Ricketts and Calvin report that the mussel crab is found in 3% of the full grown California mussels. Giles (personal correspondence) has found *F. subquadrata* in only 6 out of 805 *M. californianus* collected from Bodega Bay and Tomales Bay, California. This is less than 1% infestation. The present author has examined some 300 *M. edulis* and 104 *M. californianus* taken from the intertidal zones of San Juan Island without finding a single mussel crab.

Hart (personal correspondence) has collected

F. subquadrata from an unusual bed of intertidal *M. modiolus*. About 18% of the mussels removed from this area (located at Ten Mile Point, Victoria, Vancouver Island, British Columbia) are infested.

DISCUSSION

F. subquadrata, as do the other two pinnotherid species which have been sufficiently studied, *P. pisum* and *P. ostreum*, has a complex postplanktonic life cycle. The anomalous Stage I instar is present in the life cycle; and the prehard and posthard instars, while not identical with those of the two species of *Pinnotheres*, are quite similar. Also, as was demonstrated by Christensen and McDermott (1958:150) for *P. ostreum*, the first true crab stage following the megalops is the invasive stage.

There are extensive differences, however, between the subsequent life cycle of *F. subquadrata* and that reported for *P. ostreum* by the latter authors. Present evidence indicates that the Stage I male oyster crab must leave its host and seek out the female within her host in order to copulate. Following copulation the male leaves the female and perishes, either in the open water or within a secondary host. The results of the present study would indicate that copulation in *F. subquadrata* occurs during a freeswimming period, the swarming, in which both the male and the female participate. There is no indication that the male subsequently perishes. In fact, following the swarming period in late May and June, males are frequently taken throughout the entire summer. Wells and Wells (1961: 275) have also noted the continued persistence of males of *Pinnaxodes floridensis* following copulation.³

In addition to the copulatory swarming and persistence of the male following swarming, *F.*

subquadrata does not, at any stage in its life history, engage in the multiple infestations which occur during the early stages of *P. ostreum*.

While previous investigations (Christensen and McDermott, 1958) suggest that swarming is not typical of members of the genus *Pinnotheres*, the recent observations of swarming *P. maculatus* would indicate that at least one species of this group takes part in a copulatory swarming. It is suggested, therefore, that other pinnotherid species should be studied with regard to their reproductive behavior. This is particularly true in view of Sakai's paper (see footnote 2) in which he mentions a swarming or migration as being characteristic of the Asiatic pinnotherid, *Tritodynamia horvathi*. Miyadi (1941) has described a benthic community on the basis of a large number of pinnixid crabs found covering the bottom of certain areas of the Ise-wan, Kii Peninsula, Japan. At one station he reports that these crabs, *Pinnixa rathbuni*, occur in densities of up to 3441/m². They were found associated with several bottom types. Since he thought that such a large number of crabs cannot occupy a bottom area for an extended period of time, he suggested that among other reasons, the crabs could be "... in the reproductive period." As both *Tritodynamia* and *Pinnixa* are related in the subfamily Pinnothereliinae it is not improbable that the phenomenon observed by Miyadi was actually a swarming comparable to that observed by Sakai; and, in fact, both might be associated with reproduction. Thorson (1957:518) describes a crab community found in the Persian Gulf as being a parallel of Miyadi's community. The former community has as a dominant a pinnotherid, *Xenophthalmus pinnotheroides*, which occurs in densities of up to 1,500 mature individuals/m². Again, while Thorson suggests that this community is stable, it is not impossible that

³ While at present the genus *Pinnaxodes* is often placed in a different subfamily (the Pinnothereliinae) from both *Pinnotheres* and *Fabia* (which are in the subfamily Pinnotherinae), there is some question as to the validity of this arrangement. Rathbun (1918: 179) states that *Pinnaxodes tomentosus* "... is very likely a Pinnotheres." A thorough study of the life history of the members of this genus will possibly indicate closer affinities with the subfamily Pinnotherinae, including *Pinnotheres* and *Fabia*, than with

the Pinnothereliinae. Members of the latter subfamily, investigated in a recent study (Pearce, 1962b), as well as in the recent descriptions (Wells and Wells, 1961) of the life history and morphology of *Pinnaxodes floridensis*, differ very markedly in their life history from both *Fabia* and *Pinnotheres*. Sakai (1939:582), in his review of the Japanese Brachyryncha, placed the genus *Pinnaxodes*, along with *Pinnotheres*, in the subfamily Pinnotherinae.

the dense population observed is actually a reproductive swarming. To the present author's knowledge neither Miyadi or Thorson was able to study subsequently the respective areas, and hence it is unknown whether or not these populations were maintained.

The present investigations substantiate the finding of Christensen and McDermott (1958:174) that the soft-shelled, posthard females do not normally leave their host. As indicated earlier, however, at least the immediate posthard instars of *Fabia* are able to leave their dying host, and a small Stage V *Pinnotheres pugettensis* has been observed, and photographed, leaving its ascidian host, *Halocynthia igaboja*.

Another aspect which should be investigated further is the size differential between male and female Stage I crabs of at least two species, and the possibly related phenomenon in which males of this stage were observed to moult into soft, posthard forms as reported by the late Dr. Atkins (1958). She regarded these moults as having possible significance in the growth of male crabs. The results reported by both Christensen and McDermott (1958:153) and the present investigation indicate a somewhat larger size for the Stage I male than for the comparable female instar. The former found that the female *P. ostreum* ranges from 1.3–2.7 mm in carapace width, while the male ranges from 1.4–4.6 mm. Female *F. subquadrata* range from 1.5–6.2 and average 3.5 mm (29 individuals), while the males range from 1.3–6.8 and average 4.1 mm (54 individuals). Atkins (1958) stated that hard Stage I males would moult into a soft stage which was frequently followed by two more moults. Thus in *P. pisum*, which Atkins studied, one to three thin-shelled instars intervened between successive thick-shelled or hard forms. Since Christensen and McDermott (1958:164) were unable to keep alive the male Stage I *P. ostreum* under their laboratory conditions, they could not observe such moultings.

Male Stage I *F. subquadrata* survive in the laboratory as long or longer than the same female instar. Such a crab was taken to the Zoology Department of the University of Washington following the end of the normal summer session at the Friday Harbor Laboratories (August 30, 1959). This crab survived, in spite of

no actual feeding or efforts to maintain a normal environmental temperature, in the confinement of a finger bowl until the following spring (May 1960). Similarly, many male Stage I crabs were held throughout the summer months at the Friday Harbor Laboratories. Of particular significance was the fact that eight such crabs did moult into soft, posthard forms. It is thought that the slightly greater size of the male Stage I crabs may be a reflection of a growth moulting which has previously been regarded as anomalous or as not actually occurring.

With regard to the crab-host relationship a number of interesting conclusions can be drawn. There is no doubt that the relationship between *F. subquadrata* and *M. modiolus* is parasitic in nature, especially if the broad definition of Hopkins (1957:413) is used. The extensive, almost ubiquitous, damage to the ctenidia as well as to the underlying mantle and palps cannot be construed as anything but a result of a parasitic relationship. As with some parasitic relationships (Allee et al., 1949) it seems to have developed with a degree of specificity. By this it is meant that many species of pinnotherid crabs, including *Fabia*, are primarily found, at least in the adult instar, in a single host species. There are, however, exceptions to this generalizations, both for *Fabia* and the other pinnotherid species. Although in the waters of Puget Sound adult female *F. subquadrata* almost invariably occur in the definitive or primary host, *M. modiolus*, Wells (1928:289) reports it with both *Mytilus edulis* and *M. californianus* as well as in the branchial sac of the ascidian, *Styela gibbsii*. The crab found in the latter host was noted, however, as being immature. During the present investigation no crabs, of any stage, were found in either *M. edulis* or *M. californianus*. In the more southern extensions of its range adult *F. subquadrata* has recently been found in *M. californianus*. The status of the definitive host, *M. modiolus*, in these waters is not known.

The closely related pinnotherid, *Pinnotheres pugettensis*, which from present information may have a life history very similar to that of *Fabia*, was found only in the large ascidians, *Halocynthia igaboja* and *Ascidia paratropa*. While Wells (1928:286) reports it only from *Halocynthia (Tethyum) aurantium* collected by

Prof. Kincaid in the Friday Harbor region, the present author was unable to find it in the limited number of specimens which were available for examination. All three of these tunicates are large and quite similar in their basic morphology.

A report by McDermott (1962a:163) also contains information which indicates that, as in the *Fabia-Modiolus* relationship, the oyster crab, *P. ostreum*, may develop through the hard Stage I instar in a secondary host, *M. edulis*. After attaining the hard stage "... both sexes leave the hosts and seek some other molluscs (oysters or jingle shells) in which the females may grow to maturity." McDermott suggests, therefore, that it is possible for *P. ostreum* occasionally to utilize two hosts in completing its life cycle.

In the same paper he reported that both *P. ostreum* and *P. maculatus* are able to develop to maturity in the jingle shell, *Anomia simplex*. This is, as he notes, another new record for *P. maculatus*, and emphasizes further "... its profound lack of host specificity." This pinnotherid has previously been reported from a wide range of hosts (Rathbun, 1918:76), and since Grey (1961:357) has reported it from the tubes of *Chaetopterus* it must be assumed to be quite widely distributed.

While McDermott finds mature *P. ostreum* in *Anomia* he emphasizes that "the incidence and survival of *P. ostreum* in *Anomia* is not comparable to what we have seen in the oyster. The incidence is much lower as is its survival to maturity."

Representatives of the subfamily Pinnothereiinae, which includes the several species of pinnixids found in Puget Sound, appear to be equally specific in the selection of, or survival in, their hosts. On the tidal flats of False Bay, San Juan Island, two species of lugworm occur and each is associated with a particular species of pinnotherid crab. *Abarenicola pacifica*, a worm living in muddy sand, is almost invariably found with *Pinnixa schmitti*; while *A. vagabunda*, a species dwelling in the clean sandy bars protecting the entrance to False Bay, is usually found with *Pinnixa eburna* (Healy and Wells, 1959:325). However, Healy reports in the same paper an instance in which *A. pacifica* was found in the clean sand substrate favored by the *A. vaga-*

bunda. With three of the former worms he found *P. eburna*. Thus there is an indication that the substratum, not the worm, determines the presence of the crab. During the present investigation, however, several hundred worms of both species were subsequently checked and no anomalies were found in the crab-worm association, i.e., *P. eburna* was always found in association with *A. vagabunda* and *P. schmitti* with *A. pacifica*. One final example of the specificity of the crab-host relationship is the relationship of *Pinnixa fava* and *P. littoralis* to the large lamelli-branch host, *Schizothaerus capax*. As with *F. subquadrata*, the juveniles of these two pinnixids are found with a wide range of small bivalve species, although interestingly enough these are never the same species in which the immature *Fabia* occur. The adult *P. fava* and *P. littoralis*, however, are found only in association with *S. capax*. Even though closely related, and similar in size, *Schizothaerus nuttali* never contains the adult pinnixids and rarely the immatures. The reason for this specificity is detailed in a recent paper (Pearce, 1962b:48).

Thus, while many pinnotherid species may occasionally be found in other than the primary host during their early postplanktonic stages, the adults of most species so far studied appear typically to be found in a definitive or primary host species or type. The reasons for this specificity undoubtedly center in the fact that the crabs have evolved in many ways to fit the environment provided by a specific host organism. Apparent exceptions to the general rule, such as *P. maculatus*, must be more thoroughly investigated.

Although at the present time there is not a great body of evidence from which to extrapolate, there are indications that the pinnotherids, as a group, are actively involved in a process of adaptation. For instance, within the subfamily Pinnothereinae there is considerable variation in the use of secondary hosts. *F. subquadrata* utilizes a wide range of bivalve species, of several families, for secondary hosts although, as earlier pointed out, in the waters of Puget Sound the adults have almost invariably been found in the definitive host, *M. modiolus*.

P. ostreum, upon occasion, will infest *M. edulis* and *A. simplex* (McDermott, 1962a),

although it apparently matures only in the latter secondary host, and here there is a noticeable reduction in survival and percentage of infestation when compared to the primary host relationship with *Crassostrea virginica*. In addition McDermott (1962b:2) has observed that there are annual fluctuations in the incidence of infestation of the secondary host bivalves by *P. ostreum*, and these fluctuations should be studied to determine if there are any correlations with fluctuations or relative abundance of the primary host organism, in this case *C. virginica*.

Finally we have the case of *P. pisum* which, according to evidence presented by Christensen (1958), almost always develops, in the Kattegat, first in *Spisula solida* and then undergoes an obligatory host change to *M. modiolus*. In a more recent paper, however, Christensen (1962: 6) notes occasional exceptions to this general pattern: he has found an ovigerous female in a *Spisula* and, in addition, has found several new genera which can serve as the initial host. These are *Glycimeris*, *Cardium*, *Laevicardium*, and *Macra*.

Thus, it would appear that there is a tendency for certain species to fill several niches, at least during the juvenile stages. Whether, in an evolutionary sense, these species are progressing from an original intraspecific or single-host condition to one in which a number of host species are infested is not known. It might be suspected, however, that while the adults of many of the species thus far studied appear to be quite specific in their use of hosts, a definite advantage would accrue to a species which was able to develop in more than one host or niche. This would be especially true of forms living in tropical waters, where a greater speciation has occurred but the total number of any one species, and hence of potential hosts, might not be so great as in temperate or boreal waters. Sakai (1939:589) reports one species of *Pinnotheres* as occurring in at least five different bivalves found in Japanese waters (although there is no statement as to the stages involved); and the tropical species listed by Rathbun (1918) are frequently taken from several hosts. Again, however, there are no statements as to the stage of the crabs. It is of interest that *Pinnotheres maculatus*, which is distributed throughout a wide

range of latitude, is found in association with many different types of hosts, including polychaete worms, mussels, oysters, and scallops.

Even in temperate waters there is an advantage to the infestation of multiple host species, if only by the immature crabs. In the event of an epizootic involving the definitive host, those individual crabs which have infested the secondary hosts during the postplanktonic-hard stage of their development would still be available to reinfest the surviving, previously uninfested individuals of the primary host population.

Intergradations of morphology have been found between comparable instars of the species so far studied. Both the first crab stage and Stage I instar of *P. ostreum* have rigid, well calcified exoskeletons and possess the rod-like structures which connect the carapace to the sternum (Christensen and McDermott, 1958:150). In *Fabia* the first crab stage is not hard, while the Stage I form is; the latter stage of this species does have the well developed columnar structures linking the dorsal and ventral surfaces of the body. Similarly, in *P. pisum* the first crab stage is not hard, while the Stage I instar is.

In addition to these variations in the hosts utilized, and in the morphology of the invasive instars, there are the differences already discussed in the reproductive biology of the various species. *P. ostreum* mates within the bivalve host of the female while, from all available evidence, both *F. subquadrata* and *P. maculatus* engage in a freeswimming swarming during which copulation occurs. While nothing definite is known about this aspect of the biology of *P. pisum*, collections made by Christensen (personal correspondence) indicate simultaneous occupancy of the host bivalves by pairs (male and female) of Stage I crabs. On the other hand, the author is in possession of a female, Stage I *Pinnotheres taylora* taken freeswimming in a midwater plankton trawl.

Because of these intergradations between the various species it is extremely difficult, as suggested by Christensen and McDermott (1958: 177), to generalize in any way with regard to the biology of the pinnotherid crabs. The fact that in many species the Stage I female is modified for a freeswimming existence, and yet does

not leave the host during this phase of the development, seems incongruous. It may be that the modified morphology of the Stage I female of *P. ostreum* is an adaptation for the possible host changes which do occasionally occur in this species. Christensen and McDermott (1958:175) point out that when several female *P. ostreum* invade the same host the excessive crabs must either "perish or migrate to other oysters." According to Christensen's (1958) information on *P. pisum*, it may be assumed that this is definitely the case in this species. It seems more reasonable, however, to regard the anomalous Stage I instar, which seems common to many pinnotherids, as a remnant of an earlier ancestral life cycle in which both the male and female were hard and occasionally freeliving, and both simultaneously infested the host organism. Later, during the evolution of the group, when the symbiotic existence was definitely assumed, the female started to moult into the large soft, posthard stages capable of producing the greater number of eggs necessary to the success and survival of a cryptic, parasitic form. At the same time the male became less necessary, and today, in at least some species, seems to be eliminated following copulation. It is suggested that this is a more reasonable hypothesis regarding the evolution of these forms than that proposed by Christensen and McDermott. They state (1958:176) that posthard males, comparable to the existing female stages, probably existed somewhere in the line of evolution. Since to this author's knowledge no known males of any freeliving brachyuran species assumes the soft habitus of the posthard pinnotherid females, it seems unlikely that such males were present in the early evolutionary history of the Pinnotheridae.

Finally, as was mentioned earlier, a definite correlation has been noted between the depth from which the host mussels are collected and the percentage of infestation, as well as between depth and the size of the symbiont crabs. Possible reasons for the correlation between the depth of water in which the mussels are found and the amount of infestation have been discussed previously. It is suggested that the smaller size of the crabs taken from mussels removed from relatively deeper waters (Fig. 1) is the re-

sult of similar influences. A comparative quantitative study of the digestive tract contents of host mussels and their symbiont crabs might be of value in determining whether the limiting factors include total available food.

From the foregoing discussion it is obvious that the investigation of the family Pinnotheridae is still as desirable today as it was several decades ago, when Rathbun (1918:10) made her admonishment concerning the family. It is thought that, particularly from a systematic point of view, a more intensive comparative study of the biology of various species will produce an unsuspected amount of information. Not only will this information be of interest in itself, but it might be profitably applied to the study of benthic and pelagic communities. The effects of the symbiotic crabs on their host organisms would undoubtedly influence the role of the latter within the community. This is especially true when the host is one of the dominants within a community. In fact, *M. modiolus* has been considered a dominant organism in the *Modiolus* faciation of the *Strongylocentrotus-Argobuccinum* biome (Shelford, 1935:287) which is typical of the San Juan Channel. *Pinnotheres ostreum* has been investigated with regard to its effects on the economically important oyster beds of the east coast of the United States (Stauber, 1945; Haven, 1958). Hancock (1962) has reported that infestation by *P. pisum* reduces the average volume of the meats of the edible mussel, *Mytilus edulis*.

More recently a study has been initiated to ascertain the role which *P. maculatus* plays in the benthic mussel communities found in the waters surrounding Cape Cod and the Elizabeth Islands. Some of the preliminary results of this study are contained in this paper.

SUMMARY

1. The postplanktonic stages which succeed the megalopal instar are described and their dimensions given.

2. Like *Pinnotheres ostreum*, *Fabia subquadrata* is shown to invade the host organism during the first true crab stage.

3. "Abnormal" instars of both sexes are described.

4. The external manifestations of ecdysis in *F. subquadrata* are described.

5. Copulation occurs in open water, with both the male and female crabs leaving their symbiont host as the hard, Stage I instar. Following copulation the female crabs return to a host organism to continue their development. Some, if not all, surviving males return to a host.

6. Only during the copulatory swarming have males and females been found together. Only three multiple infestations of the host have been noted; two of these were between two males and the third was between probably incompatible stages of a male and female.

7. Copulatory swarming occurs in Puget Sound during late May. This is followed by a period of 21–26 weeks, during which the precociously inseminated females pass through the five posthard developmental instars. Ovigerous females are first noted in November; the eggs hatch in February.

8. The growth rate of *F. subquadrata* appears to be positively correlated with the growth rate of the definitive host, the horse mussel, *Modiolus modiolus*. Suggestions are given to explain the fact that immature crabs are less commonly associated with the relatively larger host mussels.

9. Four new bivalve hosts are given for *F. subquadrata*.

10. Evidence is presented which suggests that the mussel crab is a true parasite causing extensive physical damage to the host organism.

11. Crabs found in mussels removed from deeper waters tend to be smaller than those removed from hosts taken in relatively shallow waters.

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Relationships between Standing Crops at Three Successive Trophic Levels in the Eastern Tropical Pacific¹

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ABSTRACT: Measurements of the following standing crops were made at each of several pairs of stations on various cruises in the eastern tropical Pacific: (a) chlorophyll *a*, mg /m², 0–100 m; (b) zooplankton (total, and, for some cruises, copepods separately), ml/10³m³, 0–300 m; (c) small fish and cephalopods, combined, from net-caught micronekton, ml/10³m³, 0–90 m. These were considered to represent plants, herbivores, and primary carnivores. It was estimated that most of the zooplankton was located at 0–140 m. The stations of each station-pair were separated by less than 120 miles and 36 hr.

Relationships between the logarithms of crops were investigated by simple correlations, partial correlations, and structural two-variable linear regressions. In the 36 station-pairs available from cruises made in the northern spring, both zooplankton and carnivores had a significant positive regression on chlorophyll *a*; the points for 11 of these pairs fell within or close to the 95% confidence limits of each of the regressions. For these 11 "statistically selected" pairs all simple correlation coefficients were positive and significant, the partial correlation coefficient of chlorophyll *a* and zooplankton was positive and significant, and the other two partial correlation coefficients were non-significant. These results were considered to be consistent with steady-state conditions between the three standing crops. A similar analysis using copepods instead of total zooplankton gave a generally similar result. Chlorophyll *a* and primary productivity (by the C₁₄ method) were positively and significantly correlated at 19 stations where both measurements were taken.

Most of the station-pairs for which these results were obtained were located in the area bounded by 5°N, 95°W, 12°N, and the American coast (excluding the Costa Rica Dome). This is a moderately eutrophic area, where a steady state might not have been expected; however, there are indications that the process of eutrophication, which probably is vertical mixing of the upper part of the very shoal thermocline (<30 m) by wind, is itself fairly steady throughout the year. No definite indications of a steady state were obtained from any other area at any season; however, the possibility of obtaining them from more copious material is not denied.

The regression (slope) coefficients showed that standing crop of herbivores varied as some power <1.0 of standing crop of chlorophyll *a*, suggesting increasingly inefficient utilization of plants by herbivores with increase of plant standing crop. On the other hand the crop of carnivores varied in an approximately linear way with that of herbivores. The standing crop ratios, copepods/plants (by weight of carbon) and carnivores/zooplankton (by displacement volume), were both roughly estimated at 0.04 under steady-state conditions; for various reasons the corresponding food-chain efficiency ratios, for standing crops of all material at the appropriate trophic levels, would be higher.

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SPEAKING OF THE SEA, Harvey (1955) said, "In nature an equilibrium between the standing crop of plants, herbivores and carnivores is continually passing in and out of balance." He clarified this statement by reference to temporary

excesses of material at some trophic levels being causally associated with temporary deficiencies at other levels, and in so doing he summarized much observation and interpretation of standing crop changes from many investigations in temperate and cold seas.

Recently a different concept, that of a virtually undisturbed balance between standing crops of biota, has been considered applicable to tropical ocean areas. For example, Nielsen (1958) said, "A direct relationship between phytoplankton and zooplankton is normal in the sea . . . with stable hydrographic conditions such as occur mainly in tropical and subtropical regions, the standing crop of phytoplankton and its production is stable"; Holmes (1958) spoke of "a situation approaching a steady state" in regard to relationships between standing crops of chlorophyll *a* and zooplankton in the eastern tropical Pacific; Cushing (1959*a, b*) distinguished two extreme types of productive cycle, one "unbalanced" (with the features noted by Harvey) in temperate and cold seas, the other "fully balanced" or in a "steady state" (with no change in standing crops) in non-upwelling tropical regions; Menzel and Ryther (1961) found phytoplankton production and zooplankton standing crop to be rather constant over most of the year and directly related over all of it, in the subtropical Sargasso Sea. None of these authors presented data on primary carnivores.

It is important to know where and when steady states occur because they are freely incorporated in analytical models of food-chain relations concerning various parts of the ocean (Riley, 1963). At the practical level they could be of use in making forecasts.

This paper deals with statistical analysis of measurements of standing crops of phytoplankton (as chlorophyll *a*), herbivores (as total zooplankton and, in part, as copepods), and primary carnivores (as micronektonic fish and cephalopods) which were all taken together at different times and places in tropical and subtropical parts of the eastern Pacific Ocean. The object of the study was to show for which (if any) of these time-space situations all standing crop measurements were consistent with a steady-state productive cycle. It was realized that

such data could not prove the existence of such a cycle. It was necessary to make many of the measurements as opportunities offered, in the course of cruises undertaken for other purposes. The results of this work may encourage the making of additional much-needed observations of the same kind, or of better ones for the same purpose.

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MATERIAL: CRUISES, MEASUREMENTS, AND STATIONS

Cruises

Standing crops of chlorophyll *a*, zooplankton, and micronekton were measured frequently at oceanographic stations on eight cruises in tropical and subtropical parts of the eastern Pacific. On three of these cruises the observations were confined to a few small areas and do not serve the purpose of this study. The other cruises were those known as Scot (or TO-58-1) and TO-60-1, both made in the Northern Hemisphere and northern spring; Step-I (or TO-60-2), made in the Southern Hemisphere and southern spring; TO-59-1, in the Northern Hemisphere and northern winter; and TO-59-2, in the Northern Hemisphere and northern summer. Certain measurements made on these cruises were suitable for the present study in ways described below, and they are listed in Table 1.

Similar measurements of chlorophyll *a* and zooplankton, but not micronekton, were made on three other cruises, and those suitable for the present study are listed in Table 2. The cruises, known as Eastropic, Scope, and Costa Rica Dome, were all made in the Northern Hemisphere and northern autumn. Figure 1 shows the areas in which the measurements of Tables 1 and 2 were made.

TABLE 1

MEASUREMENTS OF STANDING CROPS OF CHLOROPHYLL *a* (mg/m²), ZOOPLANKTON (ml/10³m³), CAR-NIVOROUS MICRONEKTON (ml/10³m³), AND COPEPODS (ml/10³m³), AT OCEANOGRAPHIC STATIONS (stns.) IN THE EASTERN TROPICAL PACIFIC*

STN. PAIR	NOON STN.	NIGHT STN.	NOON CHLOR.	NOON ZOO.	NIGHT ZOO.	G.M. ZOO.	NIGHT MICRO.	NOON COP.	NIGHT COP.	G.M. COP.	NOTES
A. SCOT Expedition, 23 April-20 June, 1958											
1	4	3	9.7	23	24	23	2.6	0.36	1.51	0.73	
2	6	5	6.4	18	21	19	1.0	0.77	0.96	0.86	
3	8	7	14	10	20	14	3.3	0.51	0.89	0.67	
4	13	10	10	13	31	20	2.8	0.64	1.50	0.98	1
5	15	14	16	30	50	39	6.7	2.46	1.42	1.87	
6	23	27	13	79	57	67	1.0	1.89	4.52	2.92	2
7	28	29	12	49	67	57	4.4	1.67	1.94	1.80	
8	32	33	15	72	100	85	8.5	3.22	5.45	4.19	
9	34	35	12	85	84	84	4.0	7.00	6.75	6.87	
10	42	36	14	86	56	69	10.0	1.74	7.30	3.56	1
11	45	46	22	63	87	74	9.5	3.87	4.25	4.06	
12	47	48	46	100	163	131	13.9	7.85	15.06	10.87	
13	49	49	39	270	299	284	19.1	30.96	11.90	19.20	1
14	56	56	36	85	101	93	6.5	3.63	1.82	2.57	1
15	58	57	81	74	79	76	4.1	4.57	3.97	4.26	
16	60	59	41	113	148	129	7.5	5.28	3.05	4.01	
17	62	61	29	80	104	91	5.9	2.28	6.16	3.74	3
18	70	69	45	90	160	120	10.0	2.23	7.05	3.96	
19	72	71	39	130	150	140	7.9	6.63	5.49	6.03	
20	74	73	50	114	182	144	16.7	3.66	6.88	5.02	3
21	76	75	120	117	206	155	15.5	4.16	10.30	6.55	
22	79	77	49	74	111	91	24.5	0.85	6.12	2.28	
23	86	85	27	108	84	95	15.4	3.74	5.81	4.66	
24	88	90	26	127	143	135	12.7	5.77	4.26	4.96	
25	100	98	11	48	48	48	16.7	2.51	4.72	3.43	4, 5
26	122	118	23	107	122	114	13.8	6.31	7.38	6.82	5
27	139	135	37	44	52	48	14.5	2.61	4.68	3.49	5
B. TO-60-1 Expedition, 30 April-27 May, 1960											
1	20	18	11	37	77	53	1.1	1.08	5.63	2.47	
2	25	23	7.4	22	32	27	2.2	1.28	1.32	1.30	
3	31	33	6.0	56	50	53	5.5	2.72	3.70	3.17	
4	42	40	7.4	38	59	47	5.9	2.50	1.65	2.03	
5	46	44	4.8	61	63	62	4.0	1.45	2.82	2.02	
6	50	48	6.0	42	41	41	2.8	2.94	0.61	1.34	
7	54	52	9.3	68	57	62	6.8	1.42	2.68	1.95	
8	58	56	19	53	95	71	1.4	1.01	7.85	2.82	6
9	58	59	19	53	115	78	5.5	1.01	1.44	1.21	6

* In water columns or layers to about 100 m, 300 m, 90 m, and 300 m respectively, with exceptions noted; abbreviated as chlor., zoop., micro., and cop. respectively. G.M. means geometric mean. For further explanation see text and footnotes.

1. Noon and night station positions were identical.

2. No zooplankton haul was made at station 23; the value given is from an adjacent daytime station (25).

3. Micronekton net was slightly torn during the haul.

4. No zooplankton haul was made at station 98; the value given is from an adjacent night station (99).

5. Night zooplankton and night copepods were estimated as in Appendix I because the haul was shallow.

6. Same noon station was paired with two equally distant, physically similar, night stations.

TABLE 1 (Continued)

STN. PAIR	NOON STN.	NIGHT STN.	NOON CHLOR.	NOON ZOOPL.	NIGHT ZOOPL.	G.M. ZOOPL.	NIGHT MICRO.	NOON COP.	NIGHT COP.	G.M. COP.	NOTES
C. STEP-1 Expedition, 15 September-14 December, 1960											7, 12
1	1	1	12		150		3.2				1
2	3	3	18		170		8.0				1
3	4	4	11		150		10.8				1
4	8	9	15		120		11.1				
5	10	11	8.8		80		6.6				
6	16	17	3.0		20		2.3				
7	19A	19	12		60		4.4				
8	25	23	16		80		7.4				
9	28	27	34		200		1.4				
10	34A	35	5.7		50		0.6				
11	37	38	3.0		50		1.2				
12	54A	55	9.2		140		2.0				
13	58	59	7.7		40		2.7				
14	63A	64	2.4		40		1.4				
15	68A	69	2.8		10		1.6				
16	72A	73	5.0		30		4.8				
17	76A	77	4.2		50		6.1				
18	86A	85	1.8		80		5.7				
D. TO-59-1 Expedition, 15 January-25 February, 1959											12
1	2	1	24	24	47	34	12.9				5, 8
2	4	3	18	9	18	13	0.0				9
3	6	5	41	18	10	13	0.0				10
4	8	7	22	37	88	57	12.1				
5	10	9	33	111	95	103	6.6				
6	12	11	29	98	43	65	8.1				
7	23	22	21	197	396	279	6.6				
8	29	28	24	166	239	199	11.9				
9	35	36	105	196	175	185	12.1				
10	42	41	25	91	71	80	5.5				
11	44	43	30	158	77	110	9.7				
12	46	46	107	164	130	146	5.9				1
13	47	48	36	60	121	85	6.2				
14	49	50	31	54	33	42	1.4				5
E. TO-59-2 Expedition, 13 August-22 September, 1959											11, 12
1	5	2	6.6				4.3				
2	10	8	7.5				4.6				
3	16	13	16				1.4				
4	24	21	12				3.2				
5	30	32	23				31.4				
6	34	38	9.7				8.0				
7	39	42	7.6				5.1				
8	49	52	6.8				6.1				
9	55	58	12				12.7				
10	61	64	4.4				0.5				
11	73	74	11				8.0				
12	76	79	12				9.6				
13	81	82	10				8.0				

7. Chlorophyll *a* values are for a water column 0-55 m; noon zooplankton hauls were not routinely taken.
8. Noon zooplankton was estimated; see note 5.
9. No zooplankton haul was made at station 3; the value listed is an estimate (see note 5) based on the value for an adjacent station occupied on the same night on another cruise (CalCOFI cruise 5901, station 133.60).
10. No zooplankton haul was made at station 5; the value listed was obtained as in note 9, based on station 137.40 of CalCOFI cruise 5901.
11. No zooplankton data are listed because depth of haul was very variable.
12. No copepod data available.

Chlorophyll a

The standing crop of chlorophyll *a* was estimated in mg under 1 m² of sea surface for a water column 100 m deep, except for Step-I where 55 m was used. This was done by taking water samples of 3–6 liters at six to eight depths in Van Dorn closing plastic samplers; filtering, extracting from the residue, and determining chlorophyll *a* concentration in the extract by optical density measurements for each sample (Richards with Thompson, 1952); using the sample data to draw a smooth profile of chlorophyll *a* with depth, and integrating the profile with a planimeter (Holmes and Blackburn, 1960). This standing crop was considered to represent, somewhat imperfectly, the standing crop of plant material (living or dead) on which animals could feed.

Some of the chlorophyll *a* data in Tables 1 and 2 have been published previously (Holmes et al., 1957; Holmes et al., 1958; Holmes and Blackburn, 1960; Blackburn et al., 1962; Scripps Institution of Oceanography, 1960, 1961). Other

observations, including revisions of some values listed by Holmes and Blackburn (1960), are from R. W. Holmes (unpublished) and Griffiths (MS).

Zooplankton

Zooplankton was collected by making an oblique haul with an open subconical net between the desired maximum depth and the sea surface. The net was of the type that has been used for the past 15 years in the eastern and central Pacific by the Scripps Institution of Oceanography, U. S. Bureau of Commercial Fisheries (La Jolla and Honolulu), and Inter-American Tropical Tuna Commission (King and Demond, 1953); the mouth diameter is 1 m, the total length is about 5 m, and the mesh apertures are 0.65 mm wide in the front and middle sections and 0.31 mm in the rear section. The volume of water strained was estimated from readings of a calibrated flowmeter in the mouth of the net.

In making a haul, the ship steamed slowly to

TABLE 2

MEASUREMENTS OF STANDING CROPS OF CHLOROPHYLL *a* (mg/m²) AND ZOOPLANKTON (ml/10³m³) AT OCEANOGRAPHIC STATIONS (stns.) IN THE EASTERN TROPICAL PACIFIC*

EXPEDITION	STN.	CHLOR.	ZOOP.	EXPEDITION	STN.	CHLOR.	ZOOP.
EASTROPIC, November 1955 ¹	33	24	193	SCOPE, November– December 1956 ²	1	24	49
	35	22	164		2	25	37
	37	25	143		3	43	32
					4	44	54
					5	51	85
COSTA RICA DOME, November– December 1959	7	20	84	6	74	314	
	12	22	250	8	60	125	
	18	8.8	120	9	24	95	
	22	9.6	43	9C	27	250	
	26	12	100	9D	36	135	
				10	45	166	
				11	70	104	
	33	10	190	16	32	95	
	36	9.4	140	17	33	139	
	43	20	70	18	32	114	
	46	8.7	120	19	27	96	
	50–7	11	54	22	59	233	
	50–16	14	56	23	30	33	
	56	12	59	24	33	77	
				25B	49	47	

* In water columns or layers to about 100 m and 300 m respectively; abbreviated as chlor. and zoop. respectively. For further explanation see text and footnotes.

¹ Spencer F. Baird stations; station 57 was omitted, being south of Equator and remote from others in this list; chlorophyll *a* data were extrapolated to 100 m for stations 33 and 37.

² Zooplankton value for station 25A was used for the adjacent station 25B.

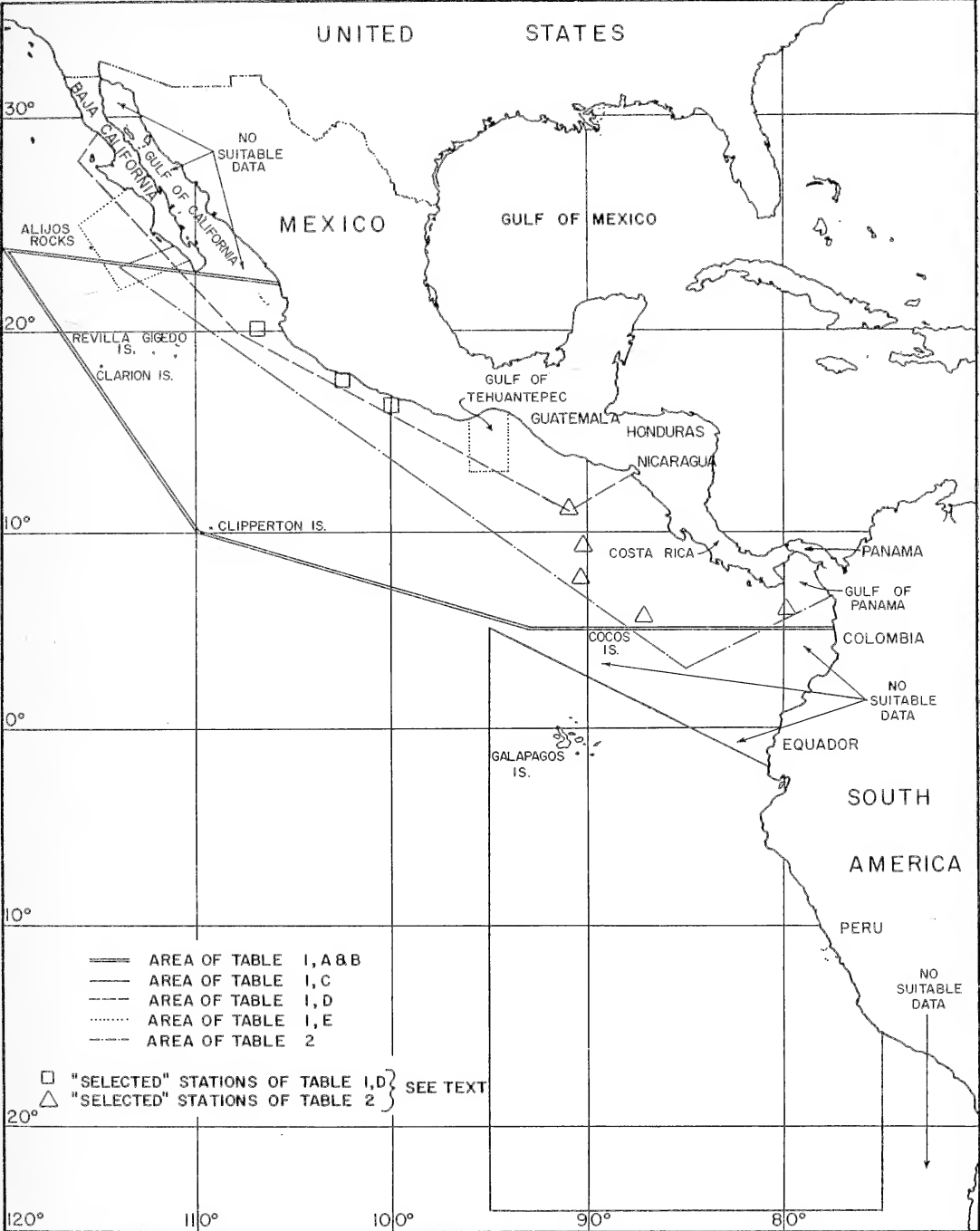


FIG. 1. Areas of groups of station-pairs and stations listed in Tables 1 and 2, and positions of "selected" stations from some groups. (See Fig. 2 for all station-pairs of Table 1, A and B.)

try to maintain a wire angle of 45° . Generally a maximum depth of 300 m was desired, but actual depths range from 203 to 401 m for hauls listed in Tables 1 and 2. At some stations identified in Table 1, the hauls were made to a desired maximum depth of 140 m (actual depths from 126 to 145 m); in each of these cases the zooplankton volume for a haul to 300 m was estimated as explained in Appendix I from the volume obtained, and the estimate (only) was listed and used in the analysis.

Measurement of standing crop was expressed as milliliters of displacement volume of the catch of small organisms (i.e., excluding organisms >5 cm in length or >5 ml in volume) per 10^3m^3 of water strained. This was regarded as a very imperfect estimate of standing crop of herbivores, because the net catches many primary carnivores but not all herbivores. An attempt to minimize these difficulties for some of the zooplankton data is described below (see section on Copepods).

Most of the zooplankton measurements in Tables 1 and 2 have been published previously (see references in section on Chlorophyll *a*, above); other observations, namely those for Table 1, B, are from Griffiths (MS).

Micronekton

Micronekton, which consists of active animals about 1 to 10 cm long, was collected with the large net and towing routine described by Blackburn and associates (1962:31–32). In brief, an oblique haul was made between 90 m (on the average; actual depths ranged from 72 to 115 m) and the sea surface, from a ship steaming at about 5 knots, with a large open subpyramidal net of uniform mesh aperture about 5.5 mm by 2.5 mm. Watery planktonic organisms were discarded from the catch, which was then sorted into its fish, cephalopod, and crustacean components; displacement volumes of these components were measured. The volume of water strained was estimated from the mouth-area of the net (2.3 m^2), the distance steamed during the haul, and a filtration coefficient of 0.757. The coefficient was measured in the way described by Blackburn and associates (1962); a subsequent experiment yielded a similar value, 0.738.

Measurements of standing crop were expressed in $\text{ml}/10^3\text{m}^3$ of water strained. For the purpose of this study only the fish and cephalopod components (combined) are considered. These may be regarded, in the main, as primary carnivores, but the crustacea are probably a mixture of herbivores, primary carnivores, detritus feeders, and omnivores; it is probable that some fish and cephalopods avoid the net. The author is responsible for these data in Table 1, none of which have been published previously in their present form.

Copepods

Measurements of standing crop of copepods from the zooplankton are available for two cruises, for which it was thought to be particularly important to have a better measurement of herbivore standing crop than that given by zooplankton. Even this measurement is imperfect, because some herbivores are excluded and some copepods are probably carnivorous. The data are from R. C. Griffiths (unpublished). They were obtained by a volumetric method, which is essentially that of Yentsch and Hebard (1957) with minor refinements (Griffiths and Fee, MS), and are expressed in $\text{ml}/10^3\text{m}^3$ of water strained. The manual sorting of copepods from the zooplankton is so time-consuming that no attempt was made to provide similar data for all cruises.

The copepod volumes are all much lower than the corresponding volumes of zooplankton (Table 1, A and B); they average 4.3% of the zooplankton and none is higher than 12%, although a figure of a much higher order was indicated by gross inspection of most of the unsorted zooplankton samples. This is clearly an effect of the different volumetric method which was used for the copepods; interstitial water is far more efficiently removed by this method than by the ordinary filtration method which was employed for the unsorted zooplankton. Possibly it is also an effect, due to shrinkage in formalin, of the later date at which the copepod measurements were made.

The volumes of zooplankton and carnivorous micronekton may not be precisely comparable either, although both were measured by the same (ordinary filtration) method at about the same

time: the former, being more heterogeneous and consisting of smaller animals (many of which have numerous appendages), probably retains more interstitial water after filtration than does the latter. Therefore these three sets of measurements lack the common biological base that the common unit, $\text{ml}/10^3\text{m}^3$, might suggest.

Stations

The standing crop of chlorophyll *a* was routinely measured at stations occupied about local noon, so that it might be compared (for other purposes) with measurements of primary production and submarine daylight; the latter are most conveniently made or started about noon. There was seldom enough time to take water samples for chlorophyll *a* at night stations, and when this was done the number of sampled depths was generally only four. On the other hand, the crop of micronekton was generally measured at stations occupied about local midnight, because of diurnal vertical migration (King and Iversen, 1962); it would have been necessary to lower the net to a much greater depth to obtain similar samples in the daytime, and time did not permit this. These and other research requirements of the cruises dictated a schedule of two major stations per day, at about local noon and midnight, on the cruises listed in Table 1. Generally a zooplankton haul was made at each of these stations except on Step-I, where it was frequently omitted at the noon station.

As a result there are no stations at which acceptable measurements of all three standing crops were made at the same time and place, although a few such sets of measurements were obtained within <36 hr at the same place (Table 1, footnote 1). For this study it was decided to pair adjacent noon and night stations which were separated by <120 miles (see numbered lines of varying length, e.g., *B1* in Fig. 2) and <36 hr. Within these limits, the stations to be paired were chosen to (a) maximize the number of station-pairs, and (b) minimize differences in time, space, and physico-chemical conditions within pairs. Five pairs were discarded because the ratio, night zooplankton/noon zooplankton, exceeded the highest such ratio observed at the same place (i.e., 2.4 for pair A4 in Table 1); it was thought that such

high ratios might signify large differences in biological conditions between adjacent stations.

The remaining 81 pairs are listed in Table 1. Zooplankton data are not given for TO-59-2 because haul depth was very variable (the ship could not maintain the desired speed). For each station-pair on the other four cruises, there are available for analysis one measurement of standing crop of chlorophyll *a*, one of zooplankton, and one of carnivorous micronekton. The zooplankton value is the geometric mean of the listed noon and night values, except for Step-I, where it is the night value.

Measurements of copepod standing crops are given for each noon and night station in Table 1, parts A and B, in the same way as the crops of zooplankton of which they formed part. The value used for each station-pair in the statistical analysis was the geometric mean of noon and night values, corresponding to the similar statistic for zooplankton. The coefficient of correlation between the two sets of geometric means is +0.881, which is significant at the 1% level of probability.

Table 2 shows only pairs of chlorophyll *a* and zooplankton measurements. Each pair refers to a single station which was occupied generally about local noon.

Positions of station-pairs and stations listed in Tables 1 and 2 may be found as follows: Table 1, A—Holmes and Blackburn (1960), also Figure 2 of this paper; Table 1, B—Griffiths (MS), also Figure 2 of this paper, also Blackburn and associates (1962, Fig. 2); Table 1, C—Scripps Institution of Oceanography (1961); Table 1, D and E—Blackburn et al. (1962); Table 2—Holmes et al. (1957) for Eastropic, Holmes et al. (1958) for Scope, and Scripps Institution of Oceanography (1960) for Costa Rica Dome.

STATISTICAL ANALYSIS: RELATIONS BETWEEN VARIABLES

General

Table 3 gives total and partial correlation coefficients among standing crops for the station-pairs of Table 1 and stations of Table 2. Parts A and B of Table 1, representing two cruises made in the Northern Hemisphere spring, have

been combined for this and all subsequent parts of the analysis. The different parts of Table 2, representing three cruises made in the Northern Hemisphere autumn, have been similarly combined. All statistics were calculated with the logarithms of the measurements; micronekton data in Table 1D were first raised by 0.1 to eliminate zeros.

The two-variable regressions given below are structural regressions fitted, estimated, and investigated by the methods of Bartlett (1949). These methods are appropriate when each variable is subject to error and when the functional relationship, rather than a predictive one, is of interest. They include the estimation of confidence limits and tests of linearity. In these regressions C, Z, M, and H are logarithms of standing crops of chlorophyll *a*, zooplankton, carnivorous micronekton, and copepods, respectively. The grouping of points for Bartlett's method was done on the basis of C values for each regression except (6), where it was done on the basis of Z values. The assumption of a linear relationship among points was validated at the 5% level of probability in each regression except (8); in (8) departure from linearity was significant at the 5% level but not at the 2.5% level.

According to Bartlett (1949), the joint confidence region for the parameters of slope and position of the above-mentioned type of regression, i.e., the region in which the true rela-

tionship is likely to lie, is elliptical. For the regressions of this paper for which such regions were of interest, it was found that the sides of the ellipses were nearly straight over most of the range of the observations, and they were accordingly drawn as straight lines in Figures 3, 4, and 5.

The positions of the regressions are of little biological interest or significance, except in a few instances mentioned in the discussion, for such reasons as: differences in amount of interstitial water included in Z, M, and H; the omission of some material of the trophic level that it was desired to measure, and/or the inclusion of some material of another trophic level, in Z, M, and H; and differences in the ways in which some crops were measured on certain cruises, namely C with respect to depth in Table 1, C and Z with respect to time of day in Table 1, C and in Table 2. However, the slopes of the regressions may be considered significant biologically, because the measurements of a given crop for a given cruise are probably all comparable, methodologically.

*Chlorophyll a, Zooplankton, and
Carnivorous Micronekton*

The largest set of data ($n = 36$) is for the combined two cruises of the Northern Hemisphere spring (Table 1, A and B). This set is henceforth called AB-36-Z. Figure 2 shows where the observations were made.

TABLE 3

TOTAL AND PARTIAL CORRELATION COEFFICIENTS AMONG LOGGED STANDING CROP DATA FOR STATION-PAIRS IN TABLE 1 AND STATIONS IN TABLE 2†

SOURCE OF DATA	n	r_{cz}	r_{cm}	r_{zm}	r_{cz-m}	r_{cm-z}	r_{zm-c}	
Table 1, A and B	36	+0.702**	+0.615**	+0.626**	+0.515**	+0.345*	+0.317	[¹]
Ditto, selected data	11	+0.966**	+0.860**	+0.840**	+0.880**	+0.348	+0.068	[²]
Table 1, C	18	+0.718**	+0.314	+0.365	+0.682**	+0.078	+0.207	
Table 1, D	14	+0.376	+0.137	+0.781*	+0.435	-0.271	+0.794**	
Table 1, E	13		+0.592*					
Table 2	35	+0.124						
		r_{ch}	r_{cm}	r_{hm}	r_{ch-m}	r_{cm-h}	r_{hm-c}	
Table 1, A and B	36	+0.613**	+0.615**	+0.602**	+0.386*	+0.390*	+0.361*	[³]
Ditto, selected data	8	+0.929**	+0.874**	+0.849**	+0.728	+0.440	+0.202	[⁴]

[¹] Series AB-36-Z

[²] Series AB-11-Z

[³] Series AB-36-H

[⁴] Series AB-8-H

† The letters c, z, h, and m indicate chlorophyll *a*, zooplankton, copepods, and carnivorous micronekton respectively, * and ** indicate significance at 5 and 1% levels of probability, and n is number of station-pairs or stations; see text for particulars of "selected data."

The correlation coefficients of Table 3 show that Z and M are independently related to C, and related to each other through their common association with C, but not otherwise. The regressions on C are

$$\begin{aligned} Z &= 1.8306 + 0.634 (C - 1.2647) = 1.0288 + 0.634 C \dots (1) \\ M &= 0.7787 + 0.668 (C - 1.2647) = -0.0661 + 0.668 C \dots (2) \end{aligned}$$

where 1.2647, 1.8306, and 0.7787 are means of C, Z, and M; the corresponding antilogarithms are 18.40 mg/m² of chlorophyll *a*, 67.70 ml/10³m³ of zooplankton, and 6.01 ml/10³m³ of carnivorous micronekton. The 95% confidence limits of the regression (slope) coefficients in (1) and (2) are 0.639 ± 0.211 (0.428 to 0.850) and 0.663 ± 0.302 (0.361 to 0.965).

The differences between such figures as 0.634 and 0.639, 0.668 and 0.663, etc., in this paper arise from features of the regression methods used by Bartlett (1949). The fitted regressions and 95% confidence limits for the regression relationships are shown in Figures 3 and 4 as solid lines and dashed lines.

Points within the confidence limits indicate the station-pairs at which the relationship between C and Z (Fig. 3), or C and M (Fig. 4), is closest to the real relationship which exists between the variables for all station-pairs. Figures 3 and 4 show several points within the confidence regions, but only three of the station-pairs represented by these points are common to both regions. For analytical purposes it was thought permissible to consider additional station-pairs, which were represented by points

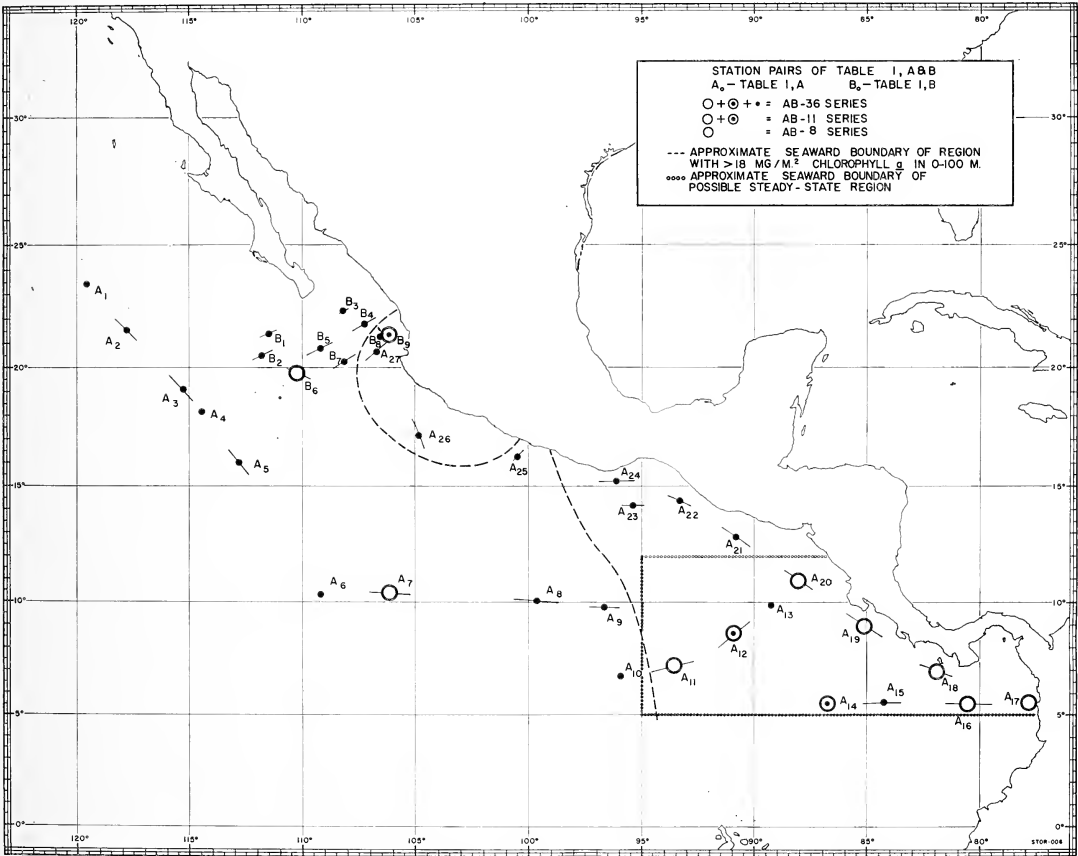


FIG. 2. Station-pairs of Table 1, A and B (Northern Hemisphere Spring), showing the series AB-36, AB-11, and AB-8, discussed in text; approximate boundaries of high-chlorophyll and steady-state regions shown.

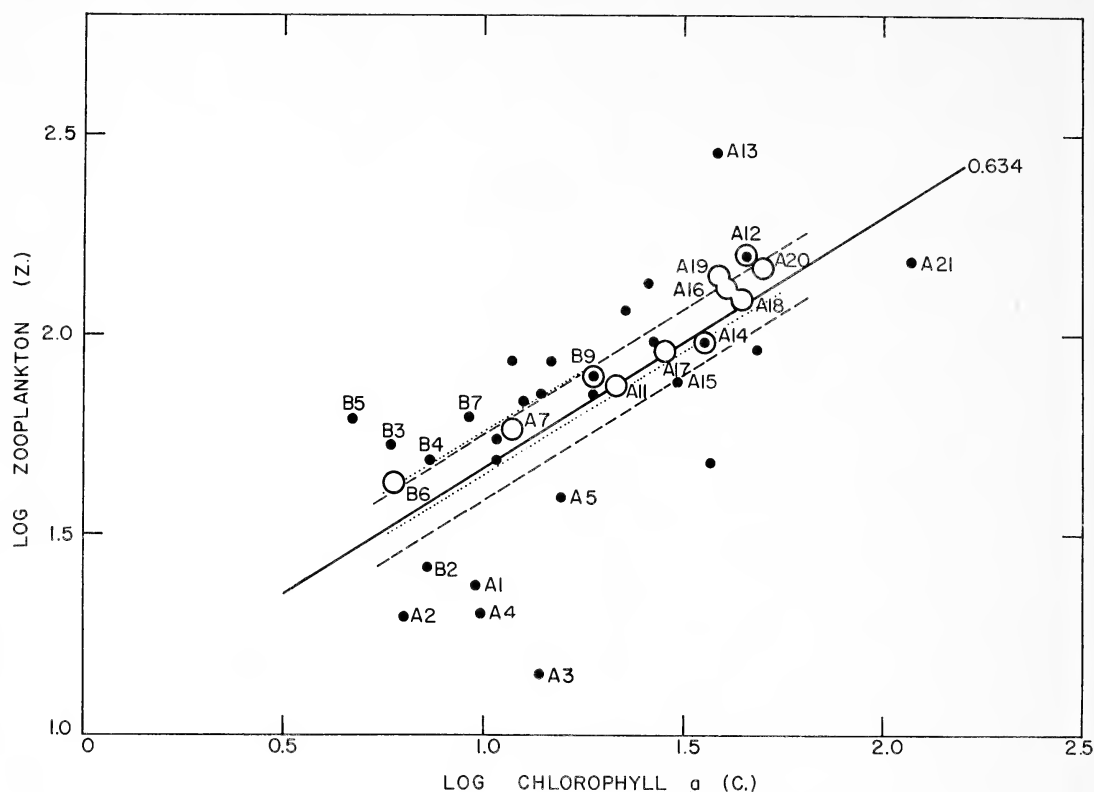


FIG. 3. Relationship between logarithm chlorophyll a (C) and logarithm zooplankton (Z) for the 36 station-pairs of Table 1, A and B (AB-36 series). Antilogarithms are in mg/m^2 over 0–100 m and $\text{ml}/10^3\text{m}^3$ over 0–300 m. Station-pairs in series AB-11 and AB-8 are identified as in Fig. 2. The solid line (—) is the fitted structural regression of Z on C and the dashed lines (---) are the 95% confidence limits of the regression, both for the AB-36 series; the dotted lines (.....) are the 95% confidence limits of a similar regression for the AB-11 series.

falling within the 95% confidence region for either of the regressions and just outside this region for the other regression. There were 8 of these, making 11 station-pairs for which the observed Z and M were both related to C in a way close to the real relationships. The set of data from these pairs is henceforth called AB-11-Z. The localities are shown by circles (with or without enclosed dots) in Figures 2, 3, and 4.

Correlation coefficients for these 11 station-pairs show that Z and M are related to C, Z independently of M, but M not independently of Z; and related to each other through their common association with C, but not otherwise (Table 3, "selected data"). The regressions on C for the 11 pairs, corresponding to (1) and (2) for 36 pairs, are

$$Z = 1.9707 + 0.619 (C - 1.4287) = 1.0863 + 0.619 C \dots (3)$$

$$M = 0.8665 + 0.666 (C - 1.4287) = -0.0850 + 0.666 C \dots (4)$$

with 95% confidence limits of the regression coefficients respectively 0.658 ± 0.152 (0.506 to 0.810) and 0.773 ± 0.522 (0.251 to 1.295). The 95% confidence limits for the regression relationships are shown as dotted lines in Figures 3 and 4.

The similarity of the two regression coefficients for AB-36-Z, and likewise for AB-11-Z, suggest a coefficient near 1.0 for the regression of M on Z. Such values (1.054 for AB-36-Z, 1.077 for AB-11-Z) are obtained when points are grouped for Bartlett's method in the same

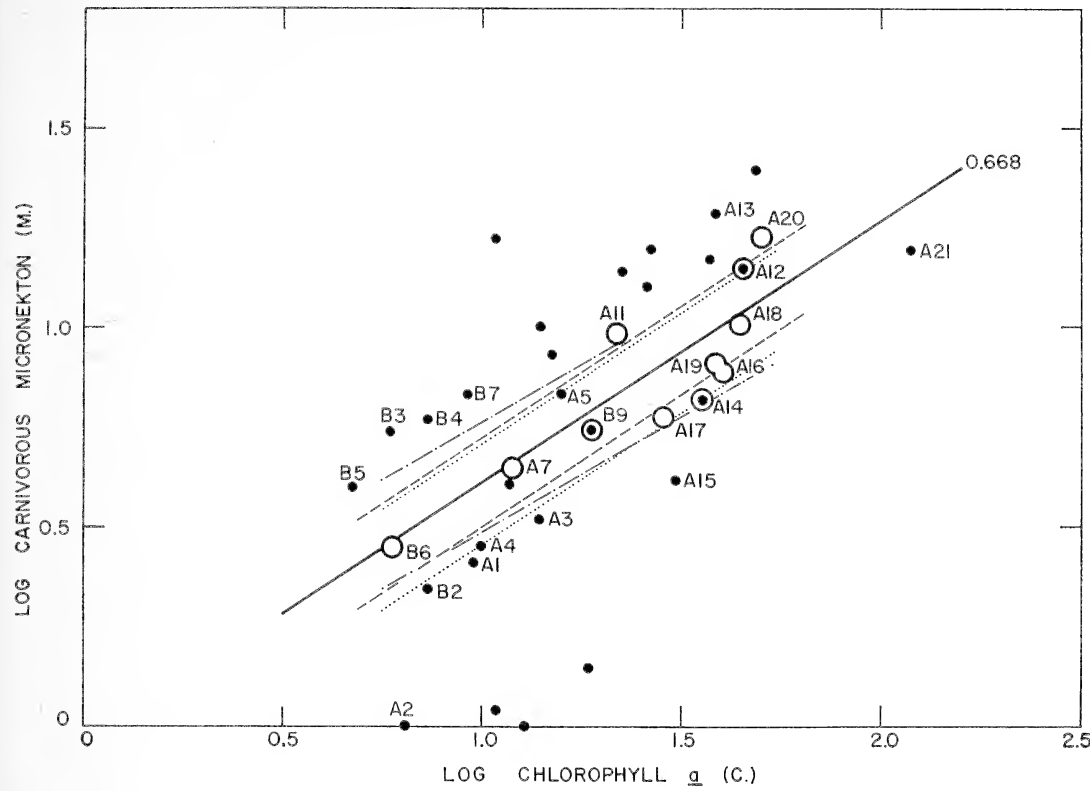


FIG. 4. Relationship between logarithm chlorophyll *a* (C) and logarithm carnivorous micronekton (M) for the 36 station-pairs of Table 1, A and B (AB-36 series). Antilogarithms are in mg/m² over 0–100 m and ml/10³m³ over 0–90 m. Station-pairs in series AB-11 and AB-8 are identified as in Fig. 2. The solid line (—) is the fitted structural regression of M on C and the dashed lines (---) are the 95% confidence limits of the regression, both for the AB-36 series; the dotted lines (.....) and dashed-and-dotted lines (-.-.-) are the 95% confidence limits of similar regressions for the AB-11 and AB-8 series.

way as for the equations above, i.e., on the basis of C values. If points are grouped on the basis of Z values the corresponding coefficients are 0.799 and 0.952.

For the less numerous data of the Southern Hemisphere spring (Table 1, C), only the regression of Z on C is significant (Table 3). It is

$$Z = 1.8153 + 0.702 (C - 0.8457) = 1.2195 + 0.702 C \dots (5)$$

where 0.8457 and 1.8153 are means of C and Z, with antilogarithms 7.06 mg/m² of chlorophyll *a* and 65.39 ml/10³m³ of zooplankton; the antilogarithm of mean M for this series of station-pairs is 3.37 ml/10³m³. Mean C is much lower than in AB-36-Z, reflecting the shorter water column over which it was measured. The 95%

confidence limits of the regression coefficient are 0.701 ± 0.359 (0.342 to 1.060).

For the still less numerous data of the Northern Hemisphere winter (Table 1, D), neither Z nor M have a significant regression on C (Table 3). This may reflect the small *n* (= 14) and the narrow range of C; the latter is 1.3222–2.0294, which may be compared with 0.2553–1.5315 for 18 differently-measured observations in Table 1, C and 0.6812–2.0792 for 36 similarly-measured observations in Table 1, A and B. The difference in range of C may be explained by the fact that the data of Table 1, D are all from inshore localities (Fig. 1); the other two series are from both inshore and offshore locations (Fig. 1), where C values tend to be high and low respectively (Fig. 2).

Since these data were obtained in exactly the same way as those in Table 1, A and B, their logarithms may be inspected to see if any of them fall within the confidence regions of regressions (3) and (4) in Figures 3 and 4. These confidence regions are considered to be more interesting than those of regressions (1) and (2), for reasons given later. The data of 3 station-pairs (numbers 5, 10, and 11 in Table 1, D; shown as "selected stations" in Fig. 1) fall within these regions, in the same way as the 11 station-pairs of the Northern Hemisphere spring.

The significant relation between Z and M (Table 3) is

$$M = 0.6018 + 1.075 (Z - 1.8586) = -1.3962 + 1.075 Z \dots (6)$$

where 1.8586 and 0.6018 are means of Z and M, with antilogarithms 72.21 ml/10³m³ of zooplankton and 4.00 ml/10³m³ of carnivorous micronekton (the last figure is 0.10 higher than the true geometric mean of micronekton values); the antilogarithm of mean C for this series of station-pairs is 32.80 mg/m² of chlorophyll *a*. The 95% confidence limits of the regression coefficient are 0.915 ± 0.816 (0.099 to 1.731).

The observations for the Northern Hemisphere summer (Table 1, E) are still fewer ($n = 13$), and for Z their quality is unacceptable; C and M are significantly related (Table 3) as

$$M = 0.7255 + 1.254 (C - 0.9910) = -0.5172 + 1.254 C \dots (7)$$

where 0.9910 and 0.7255 are means of C and M, with antilogarithms 9.80 mg/m² of chlorophyll *a* and 5.32 ml/10³m³ of carnivores; the range of C is 0.6435–1.3617. The 95% confidence limits of the regression coefficient are 1.138 ± 1.589 (–0.451 to 2.727). These limits include those of the corresponding coefficients in (2) and (4), and are too wide to have much analytical importance.

It is of greater interest to see if any of the logarithm-pairs of Table 1, E fall within the confidence region of regression (4) in Figure 4. One of them does but it may be ignored: the Z data, though imperfect, showed that the corresponding point for C and Z would probably

have fallen well outside the confidence region of regression (3) in Figure 3.

The data for the Northern Hemisphere autumn (Table 2) consist only of observations of C and Z. They are not significantly related (Table 3) despite a fairly high $n (= 35)$; possible explanations may be found in the narrow range of C (0.9395–1.8692), which probably reflects the lack of observations far offshore, and the large number of stations (about 15) located in the upwelling area of the Costa Rica Dome. Antilogarithms of mean C and mean Z are 25.02 mg/m² of chlorophyll *a* and 97.77 ml/10³m³ of zooplankton.

The Z data in this series represent noon hauls, whereas those of Figure 3 represent means of noon and night hauls. It can be shown from Table 1, A and B that the former average 0.05 less than the latter for the same station-pairs. The dotted lines representing the confidence limits of regression (3) in Figure 3 were therefore lowered by 0.05 on the Z coordinate, so that the data of Table 2 could be compared with them. It was found that the data of 5 stations of Table 2 fell within these limits: namely, Costa Rica Dome stations 22, 43, and 50–16, and Scope stations 8 and 16, which are shown as "selected stations" in Figure 1.

Chlorophyll a, Copepods, and Carnivorous Micronekton

These three standing crops (C, H, and M) can be compared only for the combined two cruises made in the Northern Hemisphere spring (Table 1, A and B). This set of data is called AB–36–H. The correlation coefficients of Table 3 reveal a set of relationships like those between C, Z, and M, except for a significant relationship between H and M which is independent of their common association with C.

Figure 5 shows the regression of H on C, corresponding to that of Z on C in (1) and in Figure 3; it is

$$H = 0.4686 + 0.652 (C - 1.2647) = -0.3560 + 0.652 C \dots (8)$$

where 0.4686 is mean H, with antilogarithm 2.94 ml/10³m³ of copepods. The 95% confidence limits of the regression coefficient are

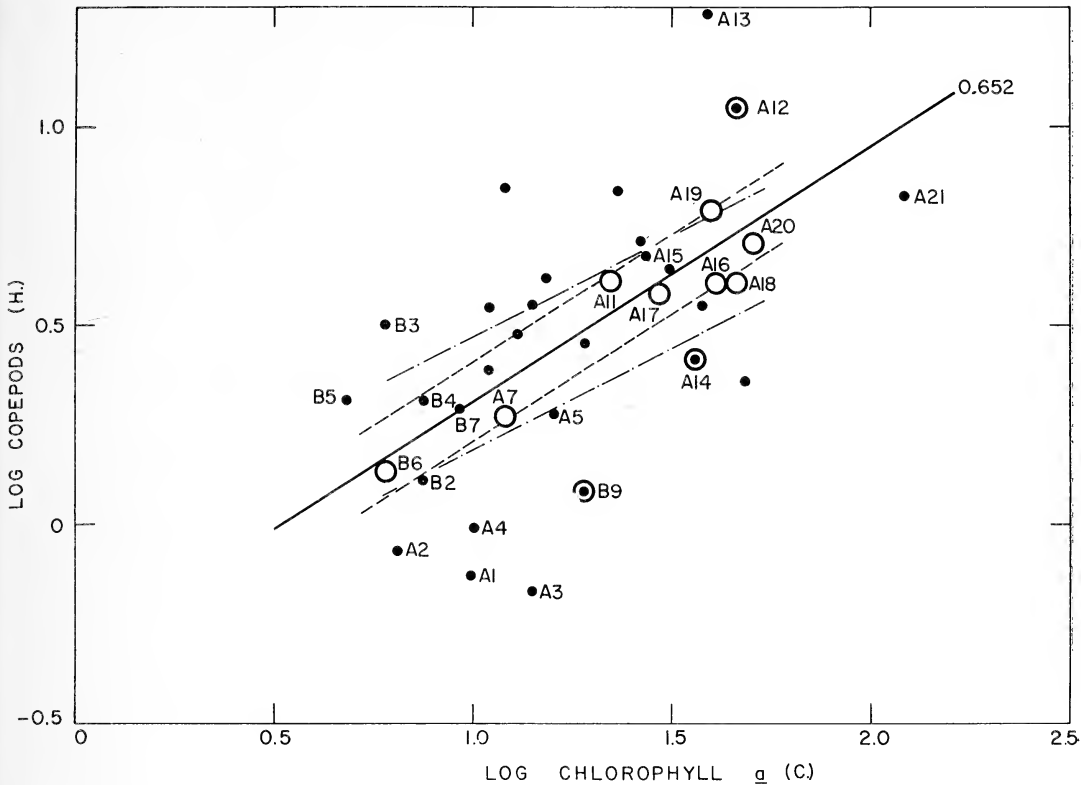


FIG. 5. Relationship between logarithm chlorophyll *a* (C) and logarithm copepods (H) for the 36 station-pairs of Table 1, A and B (AB-36 series). Antilogarithms are in mg/m³ over 0–100 m and ml/10³m³ over 0–300 m. Station-pairs in series AB-11 and AB-8 are identified as in Fig. 2. The solid line (—) is the fitted structural regression of H on C and the dashed lines (---) are the 95% confidence limits of the regression, both for the AB-36 series; the dotted-and-dashed lines (---) are the 95% confidence limits of a similar regression for the AB-8 series.

0.657 ± 0.263 (0.394 to 0.920). The fitted regression is shown in Figure 5 as a solid line and the 95% confidence limits of the relationship as dashed lines.

Points within the confidence regions of regressions (8) and (2) were compared, as described above; 8 station-pairs, for which the observed H and M were both related to C in a way close to the real relationships, were identified. They were included in the 11 station-pairs for which similar statements were made about Z, M, and C, and are identified by plain circles in Figures 2, 3, 4, and 5; the other 3 station-pairs are identified by circles with enclosed dots. This set of data, i.e., of C, H, and M from the 8 station-pairs, is henceforth called AB-8-H.

Correlation coefficients in AB-8-H (Table

3) include no significant partial coefficients, although *r*_{eh,m} is very close to significance at the 5% level of probability; all total coefficients are highly significant. The regressions on C for AB-8-H, corresponding to (8) and (2) for AB-36-H, are

$$H = 0.5308 + 0.517 (C - 1.4023) = -0.1942 + 0.517 C \dots (9)$$

$$M = 0.8543 + 0.583 (C - 1.4023) = 0.0368 + 0.583 C \dots (10)$$

with 95% confidence limits of the regression coefficients respectively 0.250 ± 0.494 (–0.244 to 0.744) and 0.558 ± 0.517 (0.041 to 1.075). The 95% confidence limits for the regression relationships are shown as dashed-and-dotted lines in Figures 4 and 5.

The similarity of the two regression coefficients for AB-36-H, and likewise for AB-8-H, suggest a coefficient near 1.0 for the regression of M on H. Such values (1.025 for AB-36-H, 1.128 for AB-8-H) are obtained when points are grouped for Bartlett's method on the basis of C values. If points are grouped on the basis of H values the corresponding coefficients are 0.701 and 1.091.

DISCUSSION

Recognition of Possible Steady-state Situations

A steady state among standing crops of phytoplankton, herbivores, and primary carnivores could be defined as a state in which material added to each trophic level (by photosynthesis, or by feeding on the level below) is continuously balanced by material lost from it (some assimilated by the level above, and some lost by other kinds of death, respiration, sinking, and active or passive emigration).

Measurements of the three standing crops in a number of different situations could be considered consistent with the steady-state hypothesis if: (i) all total correlation coefficients were positive and significant, (ii) the partial correlation coefficient of phytoplankton and herbivores was positive and significant, and (iii) the other two partial correlation coefficients were nonsignificant. In explanation of (iii), a significant positive partial correlation between phytoplankton and carnivores, independent of herbivores, would not be biologically realistic under the steady-state hypothesis; and a similar coefficient between herbivores and carnivores,

independent of phytoplankton, could signify some geographical redistribution of biota at the higher trophic levels (e.g., carnivores moving from herbivore-poor to herbivore-rich areas), and probable violation of the hypothesis.

Table 3 shows that conditions (i), (ii), and (iii) are fulfilled only for the AB-11-Z set of observations, considering all zooplankton as herbivores. Conditions (i) and (iii) are fulfilled and condition (ii) is almost fulfilled for the AB-8-H set in which copepods only were considered as herbivores; in this case the partial correlation coefficient of phytoplankton and herbivores is positive and nearly significant with only 5 degrees of freedom.

The group of 11 or 8 station-pairs represents a statistical, objective selection of a smaller set of pairs from a larger set. The data of the larger set of pairs satisfied conditions (i) and (ii) but not (iii), and it was thought that the data of the smaller set might satisfy all three conditions.

If a steady state exists, the standing crop of chlorophyll *a* might be expected to be positively correlated with primary productivity (production rate) in the same water column. This cannot be shown for the smaller group of station-pairs because productivity was estimated at only 6 of the 11 noon stations, and the incubation method and depth of sampled column were not the same for all 6. It can be shown for the 19 noon stations of Table 1, A, for which comparable water-column (0-100 m) productivity data are available (see Table 4, unpublished data from R. W. Holmes). The measurements were made by the C_{14} method using a constant-illumination "laboratory" incubator (Blackburn et al., 1962);

TABLE 4

PRODUCTIVITY (PRIMARY PRODUCTION RATE) FOR WATER COLUMN 0-100 M AT NOON STATIONS LISTED IN TABLE 1, A*

STN.	PROD.	STN.	PROD.	STN.	PROD.	STN.	PROD.
6	5.2	32	5.0	62	31.0	86	3.2
8	7.1	34	9.5	72	8.0	100	14.8
13	3.2	49	28.3	74	5.0	122	23.4
15	1.8	56	11.0	76	74.0	139**	15.0
23	11.5	58	11.8	79	10.8		

* In $\text{mgC}/\text{m}^2/\text{hr.}$; obtained by the C_{14} method, samples incubated at 1,000 foot-candles; unpublished values from R. W. Holmes, based on sample data listed by Blackburn et al., 1962, Appendix I.

** Productivity data for this station were listed for station 137 in Blackburn et al., 1962, Appendix I.

the correlation coefficient of logarithms of chlorophyll *a* and productivity is +0.532, significant at the 5% level. Estimates of water-column productivity for noon stations of Table 1, B were made using a simulated *in situ* "deck" incubator (Blackburn et al., 1962), and to a depth of only 40 m; they are not significantly correlated with chlorophyll *a* at 0–100 m ($r = +0.461$) but the data (not given here) are available for only 8 stations. It may be said that the available productivity data do not deny the existence of steady-state conditions for the station-pairs of the smaller group—at least for those listed in Table 1, A, which are all located south of 12°N.

Figure 2 shows that 8 of the 11 and 6 of the 8 station-pairs occur in the region bounded by 12°N, 95°W, 5°N, and the American coast. In this region there are only 2 station-pairs, A13 and A15, for which the standing crop data do not agree closely with the regressions describing at least one of the above-mentioned sets of data (AB–11–Z or AB–8–H). The data for A15 do not deviate much from the regressions (Figs. 3, 4, and 5). Those for A13 deviate considerably; this is not surprising because A13 is in an upwelling area, the Costa Rica Dome (Wyrski, 1964), where a steady state would not be expected.

It is clear that station-pairs fulfilling steady-state conditions were largely confined to and

characteristic of a particular ocean area, in the northern spring of 1958. It is more likely that ocean conditions permitting the existence of a steady state would be distributed in this way, than that they would occur in a number of scattered areas. This is discussed below.

It is of interest to classify the other station-pairs for which the data deviate from the regressions. For this purpose the C, Z, and M observations were used, and a station-pair was considered deviant if it fell clearly outside the confidence region of either regression (3) or (4), i.e., outside dotted lines in Figure 3 or 4. The deviations were classified as to whether Z and M values were above, within, or below the confidence limits of the regression on C. The classification of the 36 pairs of Table 1, A and B, including the 11 nondeviant ones, is in Table 5.

Table 5 shows that all but one of the possible combinations of values of Z and M (compared with C) were encountered. The most common combination was the one discussed above, with both Z and M in confidence limits (AB–11–Z); the two next most frequent combinations were those with Z and M both high, and both low, compared with C; other combinations occurred much less frequently. The station-pairs are all identified in Figure 2.

Table 5 also shows that 9 of the 11 station-pairs consistent with steady-state conditions are

TABLE 5

CLASSIFICATION OF STATION-PAIRS OF TABLE 1, A AND B (SERIES AB–36), ACCORDING TO WHETHER Z AND M VALUES FALL ABOVE, WITHIN, OR BELOW THE CONFIDENCE LIMITS OF THEIR REGRESSIONS, (3) AND (4), ON C*

Z	M	PAIRS WITH C > MEAN	PAIRS WITH C < MEAN	NO. PAIRS
Within	Within	[A11–12, A14, A16–A20] B9	A7, B6	11
Above	Above	A13, A24, A26	A8 [B3–5, B7]	8
Below	Below	A15, A21	[A1–4, B2]	7
Within	Above	A23	A10, A25	3
Within	Below	B8	A6, B1	3
Above	Within		A9	1
Below	Within		A5	1
Above	Below			0
Below	Above	A22, A27		2
TOTAL		18	18	36

* Station-pairs with C values above and below the mean are distinguished. Groups of geographically adjacent station-pairs within each class are bracketed.

in the region of higher-than-average chlorophyll *a* (Fig. 2) and account for half the pairs in this region; whereas, of the other 25 station-pairs, 16 are in the region of lower-than-average chlorophyll *a* and account for nearly all the station-pairs in that region. This is interesting because the high-chlorophyll area along the central American coast is a fairly eutrophic area; it is comparable in surface chlorophyll *a* and surface productivity with the region off southern California (Holmes, 1958). It has been supposed that steady-state conditions occur (a) in oligotrophic tropical ocean areas, but (b) not in eutrophic tropical ocean areas (Cushing, 1959*b*). The data of this paper oppose (b), and this point is further discussed below. They cannot confidently be said to oppose (a) because other relationships consistent with steady-state conditions, besides those represented by the regressions in Figures 3 and 4, could exist for certain groups of station-pairs. In this connection, Table 5 shows that 4 adjacent pairs (B3, 4, 5 and 7, all at the mouth of the Gulf of California; see Fig. 2) have high values of Z and M, whereas 5 other adjacent pairs farther west (A1-4 and B2) have low values of Z and M. Figures 3 and 4 show that the range of C is about the same for both groups. The difference between these groups might be an effect of year (the A data are from 1958, the B data from 1960) rather than of area. The matter warrants further attention when more data are available.

Station-pair A4 was off Clarion Island. This area was visited on another cruise (Island Current Survey) in May 1957, and the oceanographic data then obtained were presented by Bennett and Schaefer (1960). Chlorophyll *a* in a water column 0-80 m averaged 18.0 mg/m² for 10 offshore stations, and zooplankton (in hauls made like those described in this paper, at various times of day) averaged 16 ml/10³m³ for 10 offshore stations. The point corresponding to these measurements would fall well below the confidence region, and not far from A1-4, in Figure 3.

The productivity data of Table 4 are not obviously helpful in explaining the different kinds of deviations from regression shown in Table 5. For instance, a structural regression, fitted to the data of Table 4 and the corresponding chloro-

phyll *a* data from Table 1, A, showed that the most deviant noon stations were 15 and 76, corresponding to station-pairs A5 and A21; their productivities were respectively very low and very high for the chlorophyll *a*, but they do not help to interpret the particular combinations of C, Z, and M observed.

Biological Significance of Regression Statistics

As mentioned above, the regression (slope) coefficients are likely to have biological significance. Those involving Z or H on C are of special interest because of the many previous studies of relationships between phytoplankton and zooplankton crops. In regression (3), of Z on C, for the AB-11-Z set of station-pairs with all standing crops consistent with steady-state conditions, the point estimate of the coefficient is 0.619 with 95% confidence limits 0.506 to 0.810. In (9), H on C, for the AB-8-H set with data less certainly consistent with steady-state conditions, the corresponding figures are 0.517 and -0.244 to 0.744. Similar point estimates and confidence limits are available for three other significant regressions of Z or H on C (equations (1), (5), and (8)) in which steady-state conditions could not be demonstrated; they are respectively 0.634 (0.428 to 0.850), 0.702 (0.342 to 1.060), and 0.652 (0.394 to 0.920). Equation (1), reworked for the 27 station-pairs of Table 1, A which were all occupied in 1958, gave a point estimate 0.829 and limits 0.508 to 1.150. It may be concluded that the standing crop of herbivores generally varies with some power less than 1.0 of the standing crop of phytoplankton when there is a significant relationship between them, whether or not steady-state conditions prevail among all standing crops. This implies that herbivores utilize phytoplankton with increasing inefficiency as standing crop of the latter increases, which is consistent with the observations of some workers (Cushing, 1959*a, b*; Beklemishev, 1962; and references cited there) on excessive feeding by herbivorous copepods: when phytoplankton is abundant the herbivores may kill more of it than they assimilate.

In significant regressions of M on Z or H the coefficients are evidently much closer to 1.0 than

those for Z or H on C, as noted above, whether or not steady-state conditions prevail. For the material of Table 1, D (equation [6]), where $r_{zm,c}$ is significant, the point estimate is 1.075 with 95% confidence limits 0.099 to 1.731. For the material of Table 1, A and B, the following eight point estimates are available from various regressions noted above: 0.701, 0.799, 0.952, 1.025, 1.054, 1.077, 1.091, and 1.128. They differed in n , in the independent variable (Z or H), in the basis of point-grouping for Bartlett's line-fitting method, and in the significance of the partial correlation coefficient. It may be concluded that the standing crop of primary carnivores generally varies in an approximately linear way with that of herbivores, when there is a significant relationship between them, whether or not steady-state conditions exist among all standing crops. This means that primary carnivores utilize herbivores with about the same efficiency at different levels of herbivore standing crop.

The positions of the regressions are not nearly as informative as their slopes, for methodological reasons given above, but a few interesting comparisons of the means of paired variables can be made. Standing crops of chlorophyll *a* and copepods can be estimated very approximately in terms of a common unit, mgC/m^3 . For AB-36-H the mean crop of chlorophyll *a* is $18.40 \text{ mg}/10^2 \text{ m}^3$ in the upper 100 m, and the mean of copepods (free of interstitial water) is $2.94 \text{ ml}/10^3 \text{ m}^3$ in the upper 300 m. The latter, converted as in Appendix I, becomes $5.00 \text{ ml}/10^3 \text{ m}^3$ in the upper 140 m, and it is assumed for the present purpose that the same concentration exists in the upper 100 m. The mean amounts of chlorophyll *a* and copepods per cubic meter in the upper 0–100 m are then 0.184 mg and 0.005 ml . The latter may be taken as 0.640 mg dry weight, using the ratio of $128 \text{ mg}/\text{ml}$ given by Tranter (1960) for warm-oceanic zooplankton, predominantly copepods, free of interstitial water when measured by volume. The corresponding weights of carbon per cubic meter are estimated as 5.52 mg for the phytoplankton (multiplying weight of chlorophyll *a* by 30, after Strickland, 1960) and 0.24 mg for the copepods (considering carbon as 38% of dry weight, following Curl, 1962). The ratio, copepod C/plant

C, is then 0.043; it would, of course, be much higher for total-herbivore carbon or zooplankton carbon. It is a very rough estimate. For instance, a higher factor than 30, e.g., 60, could have been used to estimate C from chlorophyll *a* (Strickland, 1960), and the concentration of copepods could be higher in the upper 100 m than in the upper 140 m (Thraillkill, 1956); either of these could affect the ratio, although both together might not change it much. For AB-8-H the same procedures give values of 7.58 and $0.28 \text{ mgC}/\text{m}^3$, with ratio 0.037.

The standing crops of zooplankton and carnivorous micronekton cannot be expressed realistically as carbon, because of taxonomic heterogeneity and interstitial water. They can be compared in $\text{ml}/10^3 \text{ m}^3$, with many reservations. Taking Z and M antilogarithms in AB-36-Z and AB-11-Z, and estimating zooplankton in the upper 140 m as before, the following ratios (carnivorous micronekton/zooplankton) are obtained: $6.0/136.0 = 0.044$, and $7.4/191.0 = 0.039$.

The two copepod/phytoplankton and two carnivore/zooplankton ratios, one of each from a set of data consistent (or almost so) with steady-state conditions and the other not, are all about 0.04. Under steady-state conditions, ratios between total standing crops at successive trophic levels will be approximately the ratios between supplies of food available to the successive levels—i.e., "food-chain efficiency ratios," which are expected to be between 0.06 and 0.15 (Slobodkin, 1960). It is therefore emphasized for the copepod/phytoplankton ratios that the numerators, if considered to represent all herbivores, are too low. Similarly for the carnivore/zooplankton ratios, the numerators, if considered to represent all primary carnivores, are too low; the denominators, if considered as herbivores, are too high; and the denominators probably include more interstitial water, proportionate to their size, than the numerators. Thus the ratios given above are probably all too low, if considered as ratios between total crops at successive trophic levels, and need not be considered deviant from the range of expected values given above.

It is not very meaningful to make comparisons between estimates of standing crop of phy-

toplankton carbon, such as those given above, and the available data on rate of production of plant carbon. The basis for the estimates of standing crop is imperfect and most of the production data (Table 4) were obtained under nonnatural conditions of constant illumination. As a matter of interest, there are two noon stations in the AB-11 and AB-8 series, numbers 56 and 62 of Table 1, A, for which data are available for primary production rate measured by the more trustworthy *in situ* method, over the water column 0-100 m. The values are respectively 134 and 290 mgC/m²/day (Blackburn et al., 1962, Appendix I); the corresponding estimated standing crops of phytoplankton for those stations (again using Strickland's factor 30 to multiply weights of chlorophyll *a*) are 1080 and 870 mgC/m².

The difference in range of sampling depth for the three standing crops has been noted in the preceding part of the discussion. As shown earlier, the depth was approximately 0-100 m for chlorophyll *a*, 0-300 m for zooplankton (including copepods), and 0-90 m for carnivorous micronekton. Zooplankton hauls over 0-300 m have long been standard in eastern tropical Pacific investigations, in order to minimize effects of diurnal vertical migration. Data in Appendix I show that the great bulk of zooplankton at 0-300 m is actually located at 0-140 m in the eastern tropical Pacific. All standing crop measurements given in Tables 1 and 2 are, therefore, based wholly or mainly on material drawn from a water column or layer between 0-90 m and 0-140 m, with a few exceptions noted elsewhere.

Duration and Maintenance of Possible Steady State

Assuming that the standing crops of the AB-11-Z and AB-8-H data series are in steady-state conditions, the question arises as to the minimum period of time over which these conditions prevailed. This would be about the average time taken for phytoplankton material to be converted into tissue of small primary carnivores (ca. 1-10 cm), but the actual time is unknown. Blackburn (1963) assumed a period of three months in a neighboring area of the eastern

tropical Pacific, and was thereby able to relate a series of seasonal changes in properties from wind velocity to abundance of tuna. This does not justify the three-month estimate, but in fact the estimate is not unreasonable; for the Gulf of Panama, Forsbergh (1963) estimated that about two weeks might suffice for herbivores to grow from eggs to adults, and Howard and Landa (1958) showed that a small pelagic fish grows to a length of about 5 cm in between two and three months. The supposed steady-state revealed by the standing crop data in the above-mentioned series of station-pairs may therefore be considered to have lasted at least from late February to late May, when the observations were made; it could have begun earlier, ended later, or prevailed all year.

The data, then, are consistent with a steady balance between plants, herbivores, and primary carnivores, during the northern spring and possibly longer, in most of the area east of 95°W between 12° and 5°N (except the Costa Rica Dome). It might be asked how such a balance can be reconciled with the rather high standing crops and productivity observed, and other signs of biological richness such as the thick oxygen-poor layer that occurs at depth in the area (Wyrki, 1962, and references cited there). The question arises because Cushing (1959*b*) thought such biological richness in tropical areas would be seasonal, as a result of upwelling, and therefore "unbalanced" as in higher latitudes. Seasonal upwelling does not seem to explain the observations put forward here; it does occur in the northern winter and spring on the continental shelf in the Gulf of Panama (Schaefer et al., 1958), well to the north of A16 and A17 in Figure 2, but this paper does not deal with that area.

Both Cushing (1959*a, b*) and Dunbar (1960) considered other ways by which a regular supply of nutrients might be maintained in the tropical euphotic layer, such as regeneration through excretion by animals, but apparently did not consider them sufficient to maintain steady-state conditions in rich areas. This seemed to leave only upwelling, which Cushing thought would be seasonal, at least in its effects upon biota (the standing crop of phytoplankton temporarily restricted by turbulence, then increasing

with the crop of herbivores lagging behind, etc.). There are other possibilities in the part of the eastern tropical Pacific under consideration, however.

According to Cromwell (1958) and Wyrski (MS, with more abundant data) the region mentioned above is characterized by a very shoal thermocline at all times of year. The mean depth of the mixed layer is <30 m in all months, except in the southwest corner of the region (near A11 and A14, see Fig. 2) where it is >30 m (occasionally >40 m <50 m) from about August through January, and in the northwest corner (west of A13) where it is >30 m in January and February. It is <20 m in large areas of the region from about March through June, although only in small areas near the Costa Rica Dome from about October through December. It is sometimes <10 m, even in areas outside the Costa Rica Dome, and was so observed in the neighborhood of A16 at the time this station-pair was occupied in May, 1958 (Blackburn and associates, 1962, Fig. 9); a similar situation was found in about the same area in March, 1941 (Wooster, 1959, Fig. 15).

Nutrient concentrations are high in and just below the thermocline in this area (Wooster and Cromwell, 1958). As a result, nutrients are always available in the lower part of the euphotic layer, and can be supplied to the upper part of it by vertical mixing caused by wind. Such mixing probably would not carry phytoplankton below the compensation depth. Blackburn (1962) showed that gales could stir the upper part of such shoal thermoclines so as to enrich the mixed layer; the mixed layer was deepened from about 20 m to 30 m, but the thermocline was not destroyed.

The area under consideration is not very windy. No part of it has more than 20% of surface wind above force 4 Beaufort (11–16 knots) in any month, or more than 10% above force 4 in any month from March through July (Meteorological Office, London, 1956). It will be observed that winds are weakest and the mixed layer thinnest from March through July, and a little stronger and thicker during the rest of the year, as might be expected. It seems reasonable to suppose that these waters are stirred to greater than the average depth of the mixed layer when

winds of above-average velocity occur, and that this process, probably intermittent, is sufficiently regular to maintain moderate nutrient concentrations in the mixed layer during most of the year.

A steady process of upwelling might have a similar effect, and the following observations by Wyrski (unpublished) indicate the possibility of such a process occurring in the region of interest. There is an excess of precipitation over evaporation, and so an influx of high-salinity water must occur to maintain the surface salinity at the observed levels. Such water is present below the thermocline, and some of it, therefore, probably ascends.

In any event, surface concentrations of $0.50 < \text{PO}_4\text{-P} < 1.00 \mu\text{g-atm/l}$. occur in a large part of the area of interest, and concentrations $>0.25 < 0.50$ occur in the remainder of it, and these are moderately high concentrations for tropical Pacific surface waters (Reid, 1962). It appears, therefore, at least qualitatively, that a supply of nutrients can be made available to the euphotic zone in sufficient amount and with sufficient regularity to maintain steady-state conditions among the fairly high standing crops of biota in the region studied.

Nothing definite can be said about the possible effects of horizontal circulation of water in maintaining or opposing steady-state conditions in the region. Information is available on mean monthly direction and velocity of surface currents (Cromwell and Bennett, 1959), and the annual range of variation in direction has been summarized in a useful chart (Schaefer, 1962, Fig. 15). On the whole the current pattern is rather stable from month to month, except in an area between Costa Rica and Cocos Island (including A14 and A15 of Fig. 2), and it is quite possible that the effects of currents in transporting nutrients or biota are sufficiently constant over long periods to permit a steady state to exist.

The foregoing observations on physical features indicate that steady-state conditions might last all year instead of merely in the northern spring. If this were so, standing crops would probably not change much from season to season at any one place in the region of interest, although small gradual changes might occur. Un-

fortunately, insufficient data are available for comparing properties at different seasons, from this part of the eastern tropical Pacific or most other parts. The four cruises which yielded observations of the desired kind in the region between 5° and 12°N and between 95°W and the coast, were Eastropic, Scope, Scot, and Costa Rica Dome. On Scope and Costa Rica Dome the effort was concentrated in particular localities like the Costa Rica Dome, but on Eastropic and Scot it was spread rather evenly over large parts of the area. The Eastropic observations were made in November, 1955 and the Scot observations in May, 1958, and these two sets of data provide a little information about possible seasonal changes in surface chlorophyll *a* and in zooplankton at 0–300 m (Holmes et al., 1957; Holmes and Blackburn, 1960). Surface chlorophyll *a* averaged 0.28 mg/m^3 for 14 Eastropic stations and 0.29 mg/m^3 for 11 Scot stations. Zooplankton (small organisms) averaged $175 \text{ ml}/10^3\text{m}^3$ for 35 Eastropic stations and $128 \text{ ml}/10^3\text{m}^3$ for 24 Scot stations (both day and night observations included). Surface $\text{PO}_4\text{-P}$, which is also of interest, averaged $0.53 \text{ }\mu\text{g-atm/l.}$ for 18 Eastropic stations and $0.34 \text{ }\mu\text{g-atm/l.}$ for 11 Scot stations (Scripps Institution of Oceanography, 1962; Holmes and Blackburn, 1960).

This meager information suggests that no great change occurs in standing crops of biota or nutrients between one of the calmer and one of the windier months, and therefore does not deny the possibility of a steady state existing all year round. It was noted previously that the chlorophyll *a* and zooplankton standing crops for 5 Northern Hemisphere autumn stations conformed to the relationship indicated for the AB-11-Z series; all these were in the above-mentioned region of apparent steady-state, as shown in Figure 1, although several other stations from the same series in the same region did not conform in the same way. C and Z were correlated ($+0.760$, significant at the 1% level) for the 11 stations of the Northern Hemisphere autumn series (Table 2) which were in the steady-state region but not adjacent to the Costa Rica Dome.

No explanation is offered for the fact that all standing crops at a few scattered stations, west and northwest of the apparent steady-state re-

gion, conform with the relationships of the AB-11-Z or the AB-8-H series or both; these are A7, B6, and B9, among the northern spring station-pairs (Fig. 2), and D5, D10, and D11 among the northern winter pairs (Table 1, D and Fig. 1). It is worth noting that no such conformity, or any indication of steady-state conditions, was found on any cruise in Baja California (west coast) or the Gulf of Tehuantepec; physical, chemical, and biological conditions are known to vary seasonally in these regions, partly as a result of upwelling and similar processes (Reid, Roden, and Wyllie, 1958; Blackburn, 1962). No steady state was evident off the coast of Peru, an upwelling region (Wyrteki, 1963), although the useful biological data are scanty.

It is concluded that standing crops of phytoplankton, herbivores, and primary carnivores can occur off the Pacific coast of southern Central America in ways that are consistent with steady-state conditions, despite the moderately high levels of these crops. Such indications of possible steady-state conditions are lacking for other areas of the eastern tropical Pacific, which does not deny the existence of such conditions in some of these areas. More information is needed about spatial changes and especially about temporal changes in such standing crops in the eastern tropical Pacific.

Since the region off Central America has supported a successful year-round tuna fishery for many years (Martin, 1962), there are grounds for doubting the generalization of Menzel and Ryther (1961), "It is only in the inefficient eutrophic environments which irregularly produce large surpluses of basic food that large and dense populations of fishes can assemble and subsist." Eutrophic regions, including this one, probably are inefficient in the way herbivores utilize phytoplankton, but this and other features of the productive cycle may be regular and stable in some of the regions.

APPENDIX I

A station list by Klawe (1961, Table 1) enables making a comparison between volumes of zooplankton (small organisms, $\text{ml}/10^3\text{m}^3$) taken in an oblique haul to about 300 m and in a similar haul made immediately afterwards to

about 140 m, for each of 22 stations near the Revillagigedo Islands and 2 near Alijos Rocks (Fig. 1). These data were gathered on the expedition called "Tuna Spawning Survey" in July, 1957. The net and hauling procedures were as described under "Material" in this paper. The two groups of stations were evenly divided between day and night; so there were 12 of each. The published entry for station 7 gives 74.4 ml of zooplankton for the deeper haul and 52.3 ml for the shallower, but a check on the original collections showed that these entries had been reversed.

The least-squares regression of logarithm of volume from the 300 m haul (Y) on logarithm of volume from the 140 m haul (X) was obtained for the 24 stations, after analysis of covariance had revealed no significant difference between the day and night series. This regression is

$$Y = 0.0566 + 0.8009X$$

with standard error of estimate 0.130, and has been used where necessary in this paper to estimate 300 m-haul volumes from 140 m-haul volumes of zooplankton and copepods (see Table 1 and "Material"). The corresponding regression for estimating logarithm of volume of 140 m haul (Y) from logarithm of volume of 300 m haul (X) is

$$Y = 0.2059 + 1.053X$$

with standard error of estimate 0.128, and it was also used where necessary (see "Discussion").

These regressions can be used to obtain some information about the vertical distribution of zooplankton within the upper 300 m. For a range of selected values of concentration (ml/10³m³) in either the 0–140 m or the 0–300 m layer, concentrations for the other layer can be estimated. These values can be used to estimate actual volumes (milliliters) simultaneously present at 0–140 m and 0–300 m under 1 m² of sea surface, which may be called a and b. The ratio a/b is quite high even for very low concentrations (e.g., 65% where the 0–300 m concentration is 7 ml/10³m³), and it becomes 100% where the 0–300 m concentration is 42 ml/10³m³. These calculations are to some extent

unrealistic, for obvious reasons; e.g., b–a, representing actual volume at 140–300 m, becomes negative at concentrations higher than those above. They strongly suggest, however, that most of the zooplankton captured in 0–300 m hauls in the eastern tropical Pacific is located in the 0–140 m layer, especially in areas of average and high concentrations, either by day or by night.

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Observations on Osmotic Relationships in the Holothurian *Opheodesoma spectabilis*¹

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ABSTRACT: The means whereby *Opheodesoma spectabilis*, a holothurian confined to the quiet waters of Hawaii, can tolerate a dilution of 80% sea water were investigated. The animal is notable for the ratio of coelomic to tissue fluid, about 4:1.

Weight changes, osmometry, titrations, and sodium analyses on fluids before and after immersion of the animal in diluted sea water were some of the methods employed.

The animal was found to reduce its content of coelomic fluid when placed in dilute sea water for 24 hr. There is no rhythmic circulation or pumping of fluids. Water exchange and regulation of volume are by way of mouth and anus, as the body wall proved to be impermeable to water. Soluble salts of body fluids in both starved and feeding animals are below the concentrations found in sea water; but in feeding specimens, the coelomic fluid demonstrated osmotic activity approaching that of sea water.

It is suggested that tolerance to fresh water by the tissues is incidental, and derives from (1) the slow replacement of the comparatively large volume of coelomic fluid with environmental water, and (2) the habit of steady ingestion of variable quantities of organic material, leading to changing levels of digestive end-products in the coelomic fluid. Cells within the small volume of tissue fluid exchanging with the coelomic compartment can tolerate and have time to equilibrate with a wide range of concentrations, out of adaptive necessity. Volume regulation occurs in the gradual exchange between coelomic and environmental water to further advance osmotic equilibrium.

THE SEA CUCUMBER *Opheodesoma spectabilis* is a holothurian whose habitat appears to be confined to the relatively placid waters of Kaneohe Bay and Pearl Harbor of Oahu in the Hawaiian Islands (Edmondson, 1933; Fisher, 1907).

Although it is classed with the sea cucumbers, *Opheodesoma* differs from the more common types by having a thin, mucus-covered, smooth-muscle integument. This integument is usually stretched around an extraordinary amount of fluid contained in the coelomic cavity. This fluid, while it can be present in varying amounts from animal to animal and in the same animal from time to time, is most consistently found in a

ratio of about four parts to one part of tissue fluid. This comparatively large amount of mobile fluid is one of the salient features of the animal and apparently plays a significant role in its function.

In some other details of its physiology and anatomy, the animal is comparatively simple. It possesses a whorl of extensible-retractable tentacles representative of tube feet found in other echinoderms. These tentacles, usually 15 in number, surround the mouth and help the animal to ingest its food. The unconvoluted intestine, lacking the associated respiratory tree found in most other holothurians, is usually packed with a sand-algae mixture. The organic portion is digested and the end-products pass through the intestinal wall into the coelomic fluid. This fluid appears to act as the sole medium whereby nutrients are diffused to the peripherally located cell population.

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Opheodesoma may be found in large numbers quietly feeding in the shallow waters over coral reefs. During heavy rains, when large amounts of fresh water run off from land to reefs located close to shore, the animal is unaffected by influxes of fresh water that decimate populations of other reef-dwelling invertebrates.

The primary objective of this work was to establish by what means these holothurians were able to function despite marked dilution of their sea water environment from time to time.

MATERIALS AND METHODS

Animals of an average length of 45 cm were collected from the Coconut Island reef, where at low tide they can be found as little as 10 cm below the surface of the water. The animals were kept in tanks supplied with a constant flow of aerated sea water. They were starved for 48 hr prior to experimentation. This provision was thought necessary because *Opheodesoma* is a detritus-algae feeder and the animals, upon first being taken from the water, differ from each other in the amount of sand and algae present in their intestines. After 48 hr the intestines were cleared in all animals.

Preliminary experiments indicated that the animals could survive in as low a dilution as 50% sea water for at least 24 hr. However, upon being returned to 100% sea water, death usually occurred within a matter of a few days. When placed in dilutions of 80% and 70% sea water for 24 hr, then removed to 100% sea water, animals survived up to three weeks. For further experimentation 80% sea water was chosen as representing the amount of dilution the animals might naturally encounter without being irreparably harmed.

Animals chosen for study were placed one each to a 5-liter glass tank containing a known ratio of sea water to distilled water. At least three animals were used in all dilution experiments, along with three control animals in 100% sea water. The tanks were aerated and topped with aluminum foil to prevent evaporation. Immersions were for 24-hr periods. The majority of experiments were carried out at room temperatures (23°–27° C).

Evaluations of changes due to water loss or uptake were made by comparing weights before and after the experimental immersion period. Osmotically active particles present in environmental water, coelomic fluids, and tissue fluids were determined by means of a Fiske cryoscopic osmometer. Sodium concentrations were measured by means of flame photometry. Titrations for chlorosity of sea water and body fluids as a measure of salt concentration followed Knudsen's procedure (U. S. Hydrographic Office, 1955).

RESULTS

Initial experiments were devoted to determining whether *Opheodesoma* could be categorized as either an osmoconformer or an osmoregulator.

Following a 48-hr starvation period, intact animals with coelomic fluid formed while in 100% sea water were weighed and placed in 80% sea water for 24 hr (Fig. 1).

It is evident from the data that the whole animal does not act as an osmometer. On the contrary, when in environmental water more dilute than body fluids, the animals lose rather than gain weight. Apparently some form of regulation does occur which runs counter to the simple osmotic relationship that would be expected in the experiment described. That is, if the integument of *Opheodesoma* is permeable to water as described for another holothurian by

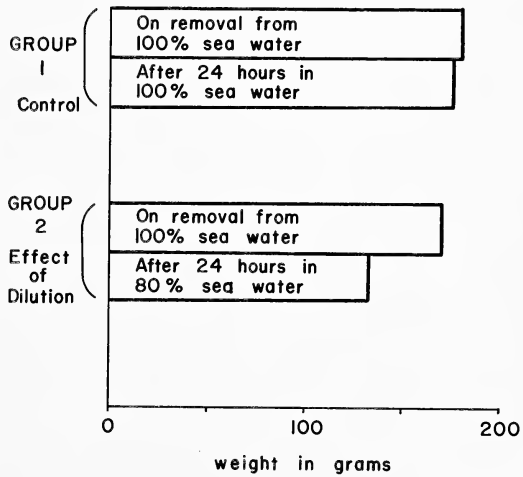


FIG. 1. Effect on animal weight after immersion in dilute sea water for 24 hr.

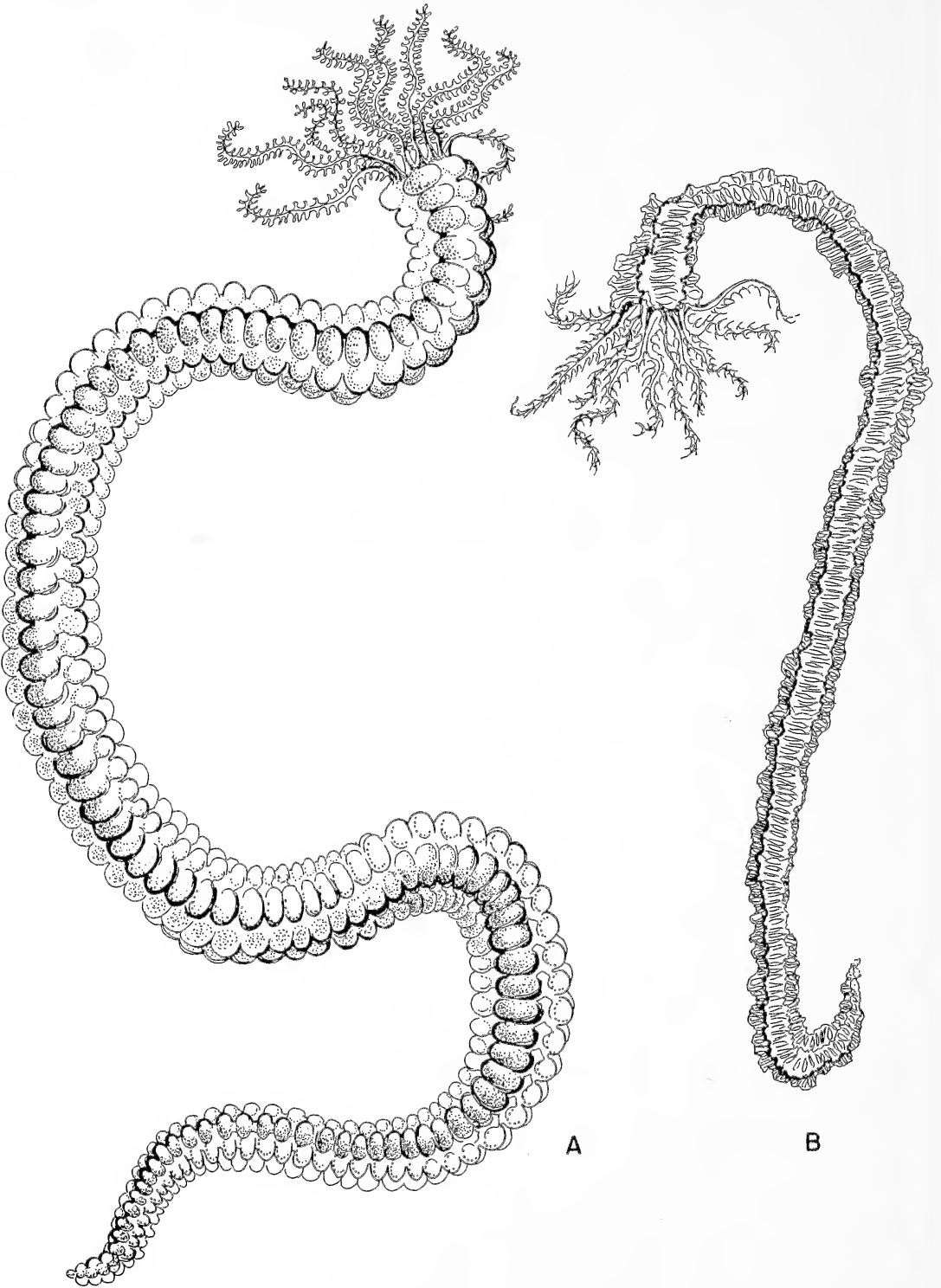


FIG. 2. *Opheodesoma spectabilis*. A, Fluid-filled state; B, drained state.

Koizumi (1935), and the body fluids are iso-motic with the sea as has been found for most marine invertebrates (Prosser, 1961), then water should follow a gradient from outside to inside.

To determine which structures are involved in passing water might provide insight into the mechanisms of water volume regulation. The most direct approach was to find the water path used by drained animals in restoring their body fluids. Draining animals is a simple but important technique which has some bearing on conclusions to be drawn later; hence, it is described in some detail.

Opheodesoma under natural conditions is in a turgid state with the body wall distended through retention of a large volume of coelomic fluid (Fig. 2A). Out of water, the animal resembles an elongated balloon. If the animal is suspended by the head, the coelomic fluid flows to the tail region; the fragile integument stretches and usually ruptures, releasing the fluid. To induce animals to drain naturally through

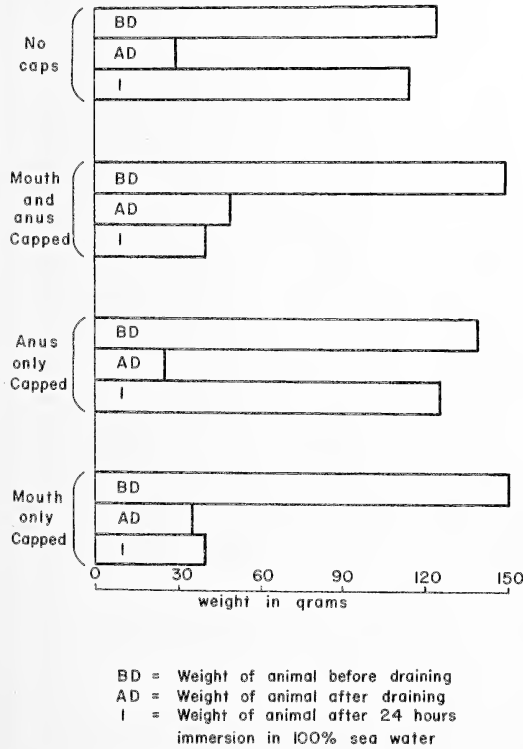


FIG. 3. Determination of functional site of water uptake in animals by use of plastic caps.

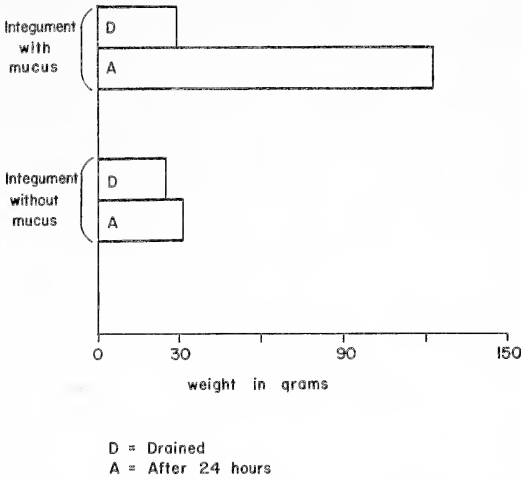


FIG. 4. The inability of animals with mucus-free integuments to restore coelomic fluid after 24 hr in 100% sea water.

the anus, they were supported in a horizontal position so that the body wall would not rupture and a 20-gauge needle was inserted carefully into the anus. Gentle manipulation with the needle usually provided the stimulation necessary to release the sphincter muscle. The fluid then would drain, leaving the animal considerably reduced in size (Fig. 2B). Upon being returned to 100% sea water, *Opheodesoma* would immediately start restoring coelomic fluid, and by the end of 24 hr it would regain an amount close to that of its original volume. If rupture of the body wall did occur at any time in the course of an experiment, the animal was discarded.

In the experiments animals were first weighed upon being removed from storage tanks. They were drained, reweighed, fitted with plastic caps in the various combinations indicated in Figure 3, and then returned to sea water for 24 hr. Water intake evidently occurs only through the mouth, with the integument acting as a water-tight barrier.

The importance of the mucus coating of the integument in making it impermeable to water was established by gently wiping off the mucus with a towel, draining the coelomic fluid from the animals, and returning them to sea water for 24 hr. As is evident from Figure 4, animals so treated usually lose the ability to regain fluid.

Volume regulation and the normal route of water exchange with the environment is via mouth and anus. But is the exchange intermittent or continuous? To test these alternatives, 1 ml of 0.1% safranin dye was injected through the body wall directly into the coelomic fluid. The animals were then washed and returned to the clear water of their natural environment in algal beds on the reef, so that feeding would not be interrupted if feeding entailed water circulation. The colored coelomic fluid could easily be seen through the semitransparent skin. During 2 hr of close observation no apparent coloring of water around the animals was detected. Removing them from the reef and draining them showed that the coelomic fluid still contained dye. Animals with coelomic fluid intact when placed in tanks containing dye-colored sea water,

showed no dye uptake after 4 hr of immersion. However, the animals were not feeding.

If water is not circulating by the mouth-anus route in a regular fashion, fluids must be "turned over" by the animals very slowly. Apparently there is no physiological demand for a constant flow of water as a carrier for oxygen or food. Oxygen could diffuse directly into and across the integument where most of the cell population is concentrated. This conclusion is supported indirectly by the fact that these particular holothurians lack the respiratory trees found in thick-walled species (Hyman, 1955).

While no direct study was made on nutritional habits, casual observation indicated an almost solid stream of sand mixed with algae being waved into the mouth by rhythmic tentacle activity. The intestine may be filled solid with

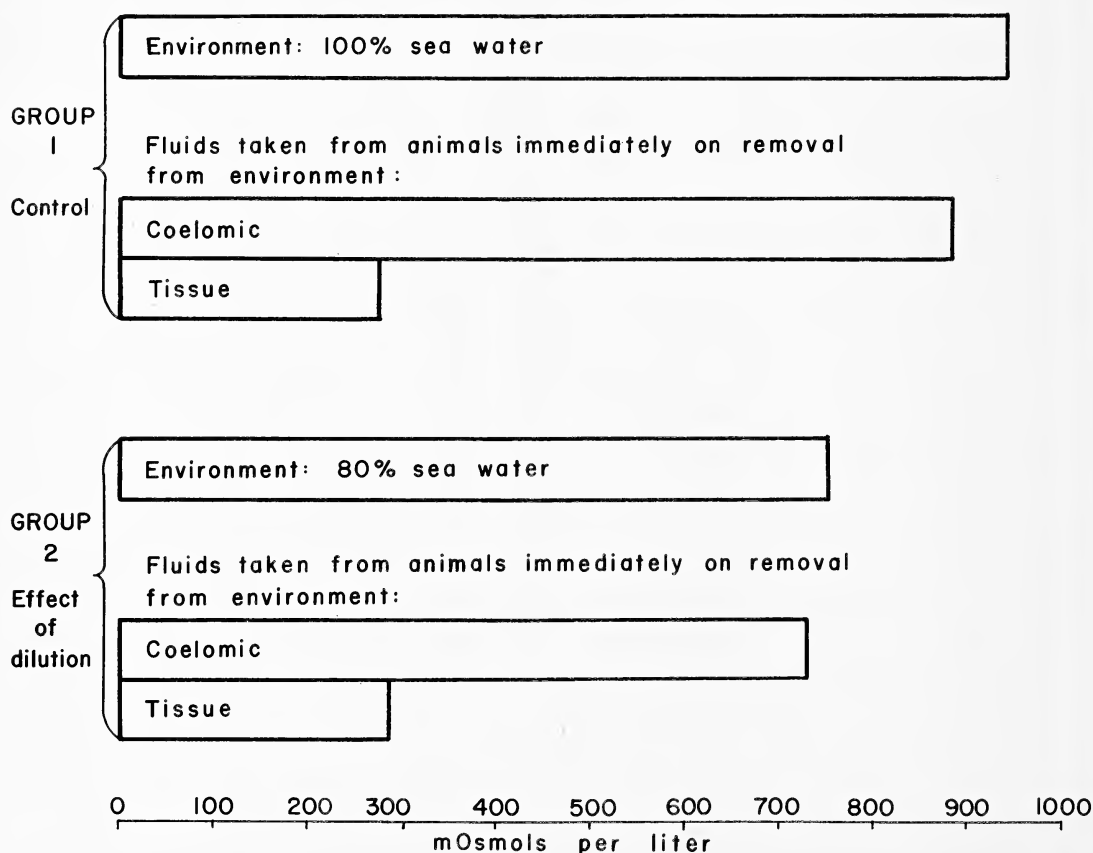


FIG. 5. The osmotically active concentrations of coelomic and tissue fluids of animals immersed in 100% and 80% sea water for 24 hr.

this mixture, while the animal is continually extruding pellets free of any vegetable matter. However, animals can vary markedly in their nutritional activity, even when lying side by side.

Evaluation was made of osmotically active substances of fluids from coelomic and tissue compartments before and after osmotic stress. For coelomic fluid determinations, draining was induced and samples were taken. Animals were either returned to 100% sea water, as in the case of the controls, or were immersed in dilute sea water. All animals were kept in tanks for 24 hr; then draining was repeated and samples were taken. Tissue fluid was obtained by drying drained animals thoroughly in toweling and then macerating them in a Waring blender. The resulting homogenate was pressed through a fine fiberglass mesh and finally filtered.

Figure 5 shows that the mOsmol values for coelomic fluids are slightly lower than for en-

vironmental water. The low concentration of tissue fluid is surprising, if it is assumed that a concentration equilibrium usually exists between body and environmental fluids in marine invertebrates. The fact that tissue fluid values are nearly the same whether or not sea water was diluted in the environment is also difficult to explain. It was hypothesized that draining the animals in the manner described might be instrumental in removing salt from the tissues. To test this possibility, coelomic fluid samples were obtained in two different ways from the same animal. One method was by draining as usual, the other was by aspiration of a small amount of fluid directly through the body wall by using a needle and syringe.

The concentrations in samples so obtained are compared in Figure 6, both in mOsmols of unspecified substances and in μ Mols of sodium. The significantly higher values of the drained

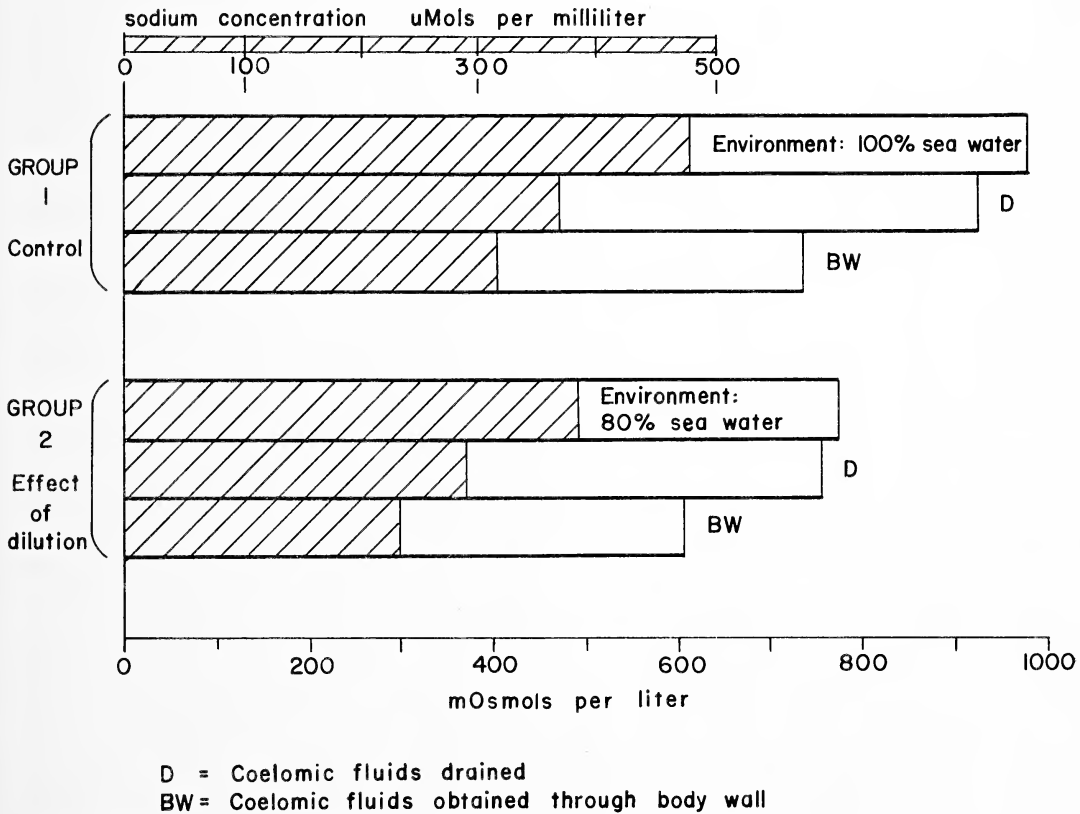


FIG. 6. Comparison of concentration of coelomic fluids obtained in two different ways. Immersion in 100% and 80% sea water for 24 hr.

TABLE 1

WEIGHT CHANGES IN ANIMALS DRAINED OF COELOMIC FLUID BEFORE AND AFTER BEING IMMERSSED
IN 100 AND 80% SEA WATER FOR 24 HR

ANIMAL NO.	INITIAL DRAINED WT AFTER REMOVAL FROM 100% SEA WATER (grams)	DRAINED WT AFTER 24 HR IN 100% SEA WATER (grams)	DRAINED WT AFTER 24 HR IN 80% SEA WATER (grams)
1	37.4	35.2	
2	31.4	29.3	
3	39.5	37.2	
4	31.0	29.2	
5	36.4		40.1
6	37.0		39.8
7	33.8		37.0
8	29.1		33.7
9	28.2		31.3

over the *in situ* coelomic samples point to a salt flow from the tissue when animals are drained. Analysis for sodium alone was done as an index to the possibility of differential ion regulation occurring between cells and coelomic fluid as an aid to osmotic balance (Robertson, 1957). The fact that sodium concentrations are propor-

tional to mOsmol values throughout indicates that ion regulation is of little importance in achieving osmotic equilibrium.

Attention was given to the wet weight of tissues as a possible quantitative index of volume regulation during stress. The data in Table 1 reveal a consistent pattern of tissues gaining

TABLE 2

WEIGHT MEASUREMENTS AND CALCULATIONS INDICATING RATIO OF SIZES
OF COELOMIC TO TISSUE COMPARTMENTS*

ANIMAL NO.	A WT WITH COELOMIC FLUID (grams)	B WT AFTER DRAINING (grams)	C WT AFTER DESICCATION (grams)	A-B COELOMIC COMPARTMENT (grams)	B-C TISSUE COMPARTMENT (grams)	RATIO OF COMPARTMENTS (COELOMIC: TISSUE)
1	165.2	39.9	2.9	125.3	37.0	3.4:1
2	134.3	24.0	2.4	114.3	21.6	5.1:1
3	156.3	29.5	2.7	126.8	26.9	4.7:1
4	124.5	33.2	2.5	91.3	30.7	3.0:1
Average	145.7	31.6	2.6	113.1	29.5	3.9:1

* One of two experiments.

water after 24 hr in dilute sea water, in contrast to the controls which lose water over the same time interval. Initially, if salt is washed out of the tissues by draining, the wet tissue weights measured after immersion in different sea water concentrations are indicative of how osmotic equilibrium may be regained. In the case of the controls, the 100% salt water is more concentrated than the washed-out tissue, and water moves out from cells. However, when the restored coelomic fluid is more dilute, the water moves from the coelomic compartment to the tissue cells.

This indicates that changes in coelomic fluid concentration can exert a sizable effect on what goes on in the tissues. This may be better appreciated by inspecting the data shown in Table 2. The amount of mobile fluid in the coelomic cavity constitutes an average of 77% of the total body weight, while the coelomic compartment itself is nearly 4 times that of the tissues. In

addition, the tissue is so arranged that most of it is stretched into a thin, membrane-like structure encompassing the coelomic fluid, so that a quick, thorough exchange between tissues and coelomic compartments is feasible.

The comparatively low concentrations found for tissue fluid might result from the imposed 48-hr starvation period. This possibility was evaluated by taking samples directly from animals feeding on the reef and comparing the concentrations with those from starved animals, by both osmometry and chlorosity titrations. Thus, osmotic activity due to salts can be distinguished from that due to organic molecules.

The data in Table 3 show that while feeding did not increase the tissue fluid mOsmol concentration, it certainly raised the mOsmol concentration of *in situ* coelomic fluid. Coelomic osmotic activity in feeding animals now approaches that of sea water but, as the chlorosity values for both feeding and starved animals are

TABLE 3

COMPARISON OF CONCENTRATIONS OF COELOMIC AND TISSUE FLUIDS IN FEEDING AND STARVED ANIMALS*

ANIMAL NO.	COELOMIC FLUID				TISSUE FLUID
	DRAINED		THRU BODY WALL		mOsmols/L
	Chlorosity†	mOsmols/L	Chlorosity	mOsmols/L	
	Feeding				
1	18.5	868	15.7	936	248
2	17.2	760	14.0	808	274
3	17.9	815	14.8	876	257
Average	17.8	811	14.8	873	260
	Starved				
4	18.8	848	13.4	587	234
5	18.7	868	13.8	664	268
6	18.0	825	14.4	697	270
Average	18.5	847	13.8	649	257

* One of two experiments.

† Chlorosity = grams of chloride per liter. Chlorosity values for tissue fluids could not be obtained due to insufficient volumes.

nearly the same, the difference can be attributed to the end products of digestion.

DISCUSSION

The easy tolerance of *Opheodesoma* to dilution of its normal sea water environment (up to 70% with no apparent harm) is puzzling. The animal has no particular structures devoted to osmoregulation; yet, the impermeability of the skin and the lack of rhythmic water circulation remove it from the category of osmoconformity. There appears to be no direct adaptive significance in tolerance extending *Opheodesoma's* environmental range. The animal is usually confined to quiet reef living, and while the ability to resist dilution may have some survival value in times of heavy rainfall for animals in shallow water, they have been found at depths up to 40 ft, presumably never exposed to fresh water.

Opheodesoma is normally a continuous ingester. This may call for a compensatory reduction in the soluble salt content of the body fluids when the organic content is high. Then the influx of digestive end-products into the large coelomic compartment raise its osmotic pressure to nearly that of sea water. Lange (1963), in his study on *Mytilus*, postulated a similar role for organic solutes acting as an osmotic buffer. Krogh (1939) cited Fredericq's finding that the tissues of certain marine invertebrates, while in osmotic equilibrium with the surrounding water, might show considerable deficit in soluble salts. This deficit is made up by organic molecules of low molecular weight.

Despite irregular water exchange with the environment and variable organic molecule levels, the volume and salt level of the coelomic fluid of *Opheodesoma* in its natural environment appear to have a certain stability. The values of the fluid samples taken through the body wall are probably more representative of actual concentrations due to the relatively undisturbing nature of the method. The inference is made here that the concentration differences between drained and *in situ* coelomic fluids must be accounted for in the tissues (Fig. 5). Consequently, the values reported for tissue fluids are lower than they actually would be *in vivo*, as measurement is possible only on drained animals. These

measurements really represent, then, a residual concentration after draining has removed some of the soluble substances which normally help keep osmotic equilibrium between tissue and coelomic fluids.

It is suggested that tolerance to fresh water by the tissues is incidental and derives from (1) the slow "turnover" of the comparatively large volume of coelomic fluid with environmental water, and (2) the habit of steady ingestion of variable quantities of organic material by the animal, leading to oscillating levels of digestive end-products in the coelomic fluid. Cells within the small volume of tissue fluid exchanging with the coelomic compartment have time to equilibrate with a range of concentrations, and can tolerate them out of adaptive necessity.

Submitting *Opheodesoma* to dilutions of sea water of the order they might naturally encounter in terms of fresh water runoff creates no critical problem, particularly when ingestion is slowed or stopped. The resulting reduction in the level of organic molecules in coelomic fluid would lower its osmotic activity. New osmotic equilibrium would be established between tissue and coelomic fluids. Then, as gradual exchange between coelomic and environmental water occurs via the mouth-anus route, reduction of coelomic volume follows as a necessary condition for complete osmotic equilibrium.

ACKNOWLEDGMENTS

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Ellobiopsidae of Alaskan Coastal Waters

ETHELWYN G. HOFFMAN and ROBERT M. YANCEY¹

ABSTRACT: Four species of ellobiopsids were taken in Alaskan coastal waters. *Thalassomyces fagei* (a synonym of *Amallocystis fagei*) was found to parasitize specimens of the euphausiid *Thysanoessa raschii* taken in Kachemak Bay, Alaska. The development of *T. fagei* external to the host from a small knob to the mature form was found to occur by repeated dichotomous branching. *T. fagei* occurred during April and May but was not observed at other times of the year. *Thalassomyces* sp. was found to be parasitic on specimens of the mysid *Acanthomysis pseudomacropsis* taken in Kachemak Bay, Alaska. The range of *Thalassomyces capillosus*, parasitic on the caridean *Pasiphaea pacifica*, is extended from Coos Bay, Oregon, to Orca Bay, Prince William Sound, Alaska. *Ellobiopsis chattoni* was found to parasitize the copepod *Metridia longa*, a new host of this ellobiopsid. Specimens of *E. chattoni* were taken in the waters of southeastern Alaska, extending the range of *E. chattoni* from the Atlantic to the north Pacific.

THE SYSTEMATIC POSITION of the family Ellobiopsidae Coutière and the genera therein has been an enigma since their original description. According to Margaret Jepps (1937), T. Scott in 1897 first described the ellobiopsid now known as *Ellobiopsis chattoni* as a "? infusorian parasite" of the copepod *Calanus finmarchicus*. She states also that in 1910 Caullery associated the ellobiopsids with the Dinoflagellata. Various authors have continued to consider these organisms to be closely related to the dinoflagellates. Jepps points out that a relation with the fungi is possible. Boschma (1949, 1956, and 1959) reviewed the entire group and preferred to consider them as "Protista of uncertain position." He noted that the ellobiopsids have affinities with the following groups: parasitic peridinians, flagellates, and possibly fungi of the family Saprolegniaceae, and that the group is made up of a number of heterogeneous elements.

The family Ellobiopsidae is a rather heterogeneous group consisting of several genera. Members of the genus *Ellobiocystis* are epibionts, whereas members of the genera *Ellobiopsis* and *Thalassomyces* are parasites. This study is concerned only with the last two genera.

Various pelagic crustaceans, including copepods, euphausiids, and carideans, are hosts of species of *Ellobiopsis* and *Thalassomyces*.

Organisms of the genus *Ellobiopsis* parasitize several species of copepods. Various species of *Calanus* have been reported by Marshall et al. (1934), Marshall and Orr (1955), and Jepps (1937) to be parasitized by *Ellobiopsis chattoni*. *Pseudocalanus* (Marshall, 1949), *Clausocalanus* (Hovasse, 1951), *Acartia* (Boschma, 1956), and *Metridia*, in this work, have also been found as hosts of *E. chattoni*.

Jepps (1937) described very early forms of this parasite which she found on the antennae and mouth parts of *Calanus finmarchicus*. These first appeared as small knobs on the setae of the mouth parts. At maturity *E. chattoni* consists of a pear-shaped part, the trophomere, which is attached by a stalk to the host's appendage. Distal to the trophomere there may develop one or two rounded segments, the gonomeres, in which sporulation takes place. According to Jepp's description of sporulation in *E. chattoni*, small buds arise on the free surface of the gonomere, each of which undergoes a series of fissions, forming spores. The mechanism of spore release and the relation between free spores and the occurrence of small knobs on the host appendages is unknown.

¹ U. S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. Manuscript received August 20, 1964.

Species of *Thalassomyces* (formerly known as *Amallocystis*) are different in many respects from those of *Ellobiopsis*. Each *Thalassomyces* consists of a tuft of trophomeres extending from a central stalk, whereas each *Ellobiopsis* has only one trophomere. The number of trophomeres extending from the stalk is used as a species-differentiating character in *Thalassomyces*.

The gonomere (or gonomeres) which forms on the distal end of the trophomere is separated by a septum from the trophomere. Individuals of *Ellobiopsis* species have one or two gonomeres. If more than one gonomere is present, as in the *Thalassomyces* species and some *Ellobiopsis* species, each is separated from the next by a septum. Sporulation has not been described for any *Thalassomyces* species but is assumed to occur. Old individuals of *Thalassomyces* spp. may be found with numerous empty gonomeres; some with collapsed walls may remain attached to the trophomere.

Various euphausiids, mysids, and carideans have been reported as hosts for *Thalassomyces* species. The ellobiopsid may be attached ventrally to the host's abdomen, as in *T. racemosus*, to the dorsal surface of the carapace, as in *T. fagei* and *Thalassomyces* sp., or at the base of the rostrum, as in *T. capillosus* (Boschma, 1956).

As a result of this study the ranges for three species of ellobiopsids have been extended to Alaskan waters. They are *T. fagei*, *T. capillosus*, and *E. chattoni*. *T. capillosus* is the only species of the three previously recorded in the north Pacific Ocean. The development of *T. fagei* is described, and seasonal distribution of this species is discussed. *Metridia longa* was found to be a host for *E. chattoni*.

OBSERVATIONS AND DISCUSSION

Thalassomyces fagei

The genus was named *Amallocystis* until 1959, when Boschma pointed out that, because of its priority, *Thalassomyces* is the valid name.

The euphausiid *Thysanoessa raschii* (M. Sars) has been recorded as host for this ellobiopsid on two previous occasions. Einarsson (1945) described *Amallocystis* sp. parasitic on *T. raschii* taken in May in Faxaflói to the west of Iceland.

Boschma (1949) established that the *Amallocystis* sp. of Einarsson was *A. fagei* (Boschma), and later (1959) he corrected the generic name to *Thalassomyces*. Glover (1952) observed two specimens of this euphausiid infected with *T. fagei*. One was taken in July and the second in August of 1948 in the region of May Island in the Firth of Forth. Initially *T. fagei* (Boschma) was described as an Antarctic species, but its distribution has been extended to include the northern Atlantic waters by reports of Einarsson (1945), Glover (1952), and Macdonald (1927). Macdonald reported the occurrence of *Staphilocystis racemosus* on the euphausiid *Meganyctiphanes norvegica* taken in the Clyde Sea. Boschma (1949) believes that this ellobiopsid was *T. fagei* and not *S. racemosus*.

In our investigation we also found *T. fagei* parasitic on *Thysanoessa raschii*. The specimens were taken during the spring of 1963 in three small inlets which are part of Kachemak Bay, Alaska (59°27'N, 151°33'W). The samples were taken in 20-minute oblique hauls of a 1/2-m plankton net with a standard No. 2 mesh. The depth in the area did not exceed 53 fathoms. This is the first record of this species of ellobiopsid from the Pacific Ocean, and its range is thus extended from the Atlantic to the north-eastern Pacific.

The ellobiopsid parasites are attached to the host by a stalk which extends through the dorsal side of the carapace and penetrates the tissues below. The parasite is located in a dorsal concavity on the carapace of the host which is not found in uninfected euphausiids (Fig. 1). An infected *T. raschii* usually bears only one *Thalassomyces*, although up to four were observed. A specimen bearing two parasites is shown in Figure 2.

The mature parasite has 30–50 trophomeres which are ramifications of the single central stalk. The trophomeres are expanded distally into a club shape. Trophomeres with one to six gonomeres were observed, although more commonly three to five occur. The gonomeres are spherical to slightly elliptical in shape. Figures 3 and 4f are a photograph and a camera lucida drawing respectively of a mature parasite. In older individuals some of the distal gonomeres are empty. The gonomere remnant may break

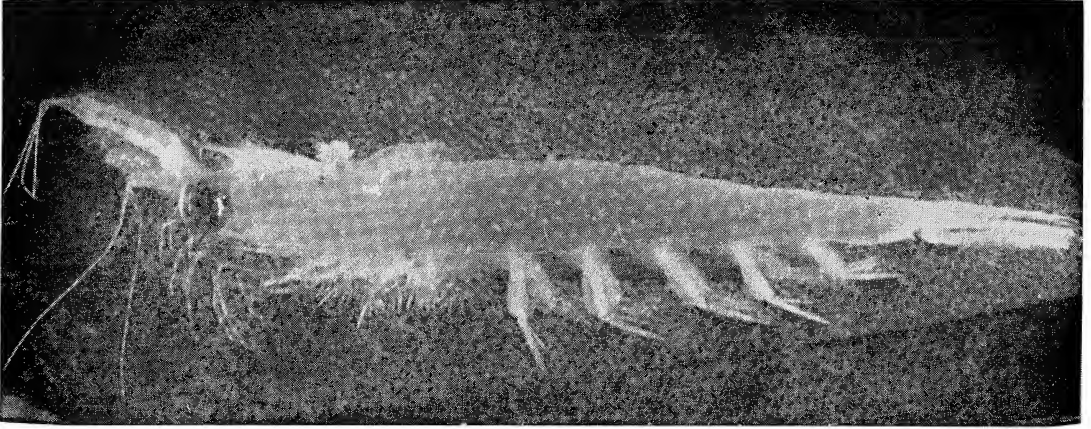


FIG. 1. A young ellobiopsid located in a concavity on the dorsal side of host's carapace.

off, leaving a small tuft, or the walls may collapse, producing a filament hanging from the end of a more proximal gonomere (Fig. 4f). Jepps (1937) has observed that in *Ellobiopsis chattoni*, parasitic on *Calanus finmarchicus*, this condition of the gonomere is the result of sporulation. She noted that when all the spores have been released, the test of the distal segment either degenerates or is left full of debris.

The development of *Thalassomyces fagei* was worked out from a sequence of specimens taken in various stages of growth (Fig. 4). The ellobiopsid was removed from its host and placed with the stalk extending upward to facilitate drawing. The illustrations show this aspect of the parasite, except Figures 4a and 4b, which are views from one side. All the drawings were done with the aid of a camera lucida.

It is not known whether the initial infection by the parasite is located internally or externally. Jepps (1937) hypothesized that *E. chattoni* initially penetrates the host from the outside. In the material of *Thysanoessa raschii* examined in the present study, *Thalassomyces fagei* was found to have a well-established internal structure at the earliest stages in its external development. Figure 4b is a lateral view of *T. fagei* shown extending through the host carapace. The structure in the lower left is the "sieve plate" of Boschma (1949). Numerous protoplasmic excrescences protrude through openings in the cuticle of the ellobiopsid. These excrescences are thought to be the organ of absorption of food for the parasite.

The major function of the external structure of the parasite is assumed to be reproductive.

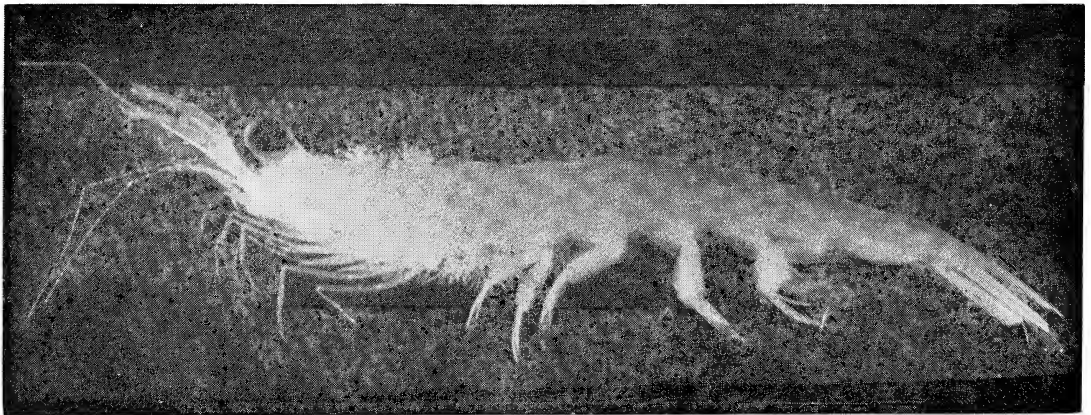


FIG. 2. Euphausiid with two discrete parasites.

Whether reproduction is sexual or asexual is unknown. These observations agree with the hypothesis accepted by Boschma (1949) for *T. fagei* concerning the assumed release of spores from the gonomere. Jepps (1937) described sporulation in the distal structure which she termed the gonomere of *Ellobiopsis chattoni*. Hovasse (1951) observed sporulation of *E. fagei*. No observations of sporulation in a *Thalassomyces* species are available.

The external development of *T. fagei* is initiated by a small knob-shaped structure appearing through the middorsal region of the carapace of the host. This single knob bifurcates slightly, producing a bilateral structure (Fig. 4a). The next stage appears to be the result of simultaneous bifurcation of each of the previously formed lobes, resulting in a four-lobed structure (Fig. 4c). Further development of *T. fagei* is accomplished by repeated simultaneous dichotomous branching of each of the existing lobes. The simultaneous nature of the bifurcation is retained until the fifth or sixth division at which time the branching appears to get out of phase.

In this study 77 specimens of *T. fagei* were examined. These were taken in plankton samples from three stations located in the Cook Inlet area of Alaska. The locations of the stations were as follows: at the mouth of Kasitsna Bay ($59^{\circ}28.7'N$, $151^{\circ}33'W$) and two stations in Tutka

Bay ($59^{\circ}26.5'N$, $151^{\circ}22.7'W$, and $59^{\circ}25.5'N$, $151^{\circ}19.5'W$).

The seasonal distribution of *T. fagei* was found to coincide in part with that reported for the same species parasitic on *Thysanoessa inermis* by Einarsson (1945). He found *Thalassomyces fagei* (as *Amallocystis* sp.) on mature euphausiids during May only. In our work during February and March of 1963 numerous *Thysanoessa raschii* were observed, but most of the individuals taken during this time were juveniles. Early stages of *Thalassomyces fagei* first appeared on the host early in April, 1963. Mature ellobiopsids were taken from late April until about the first of June. The external structures of *T. fagei* were not present on the euphausiids taken in February or March, nor were they present late in June. During May, 1963 we noted 13% average infection of *Thysanoessa raschii* by *Thalassomyces fagei*. This was based on three samples containing 239 specimens of *Thysanoessa raschii*, of which 33 were parasitized.

It appears unlikely, at least from the preserved material, that a mature *Thalassomyces fagei* could pass through the hole in the carapace of the host at molting. This is due to the fact that the host's exoskeleton closely surrounds the stalk of the ellobiopsid. Since euphausiids have a high intrinsic rate of molting, one can assume either that the euphausiids continue to molt with their

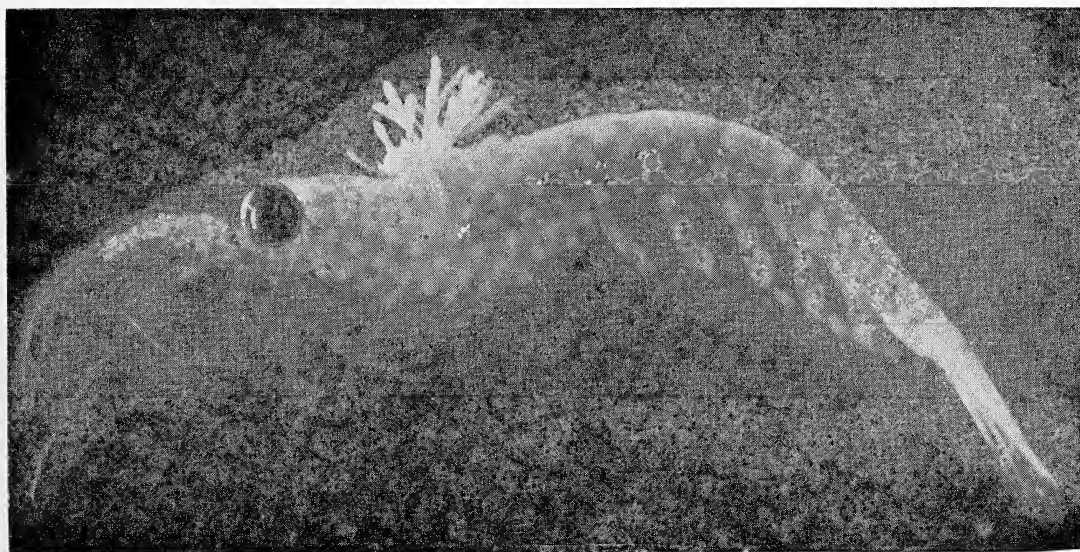


FIG. 3. Euphausiid with a mature parasite.

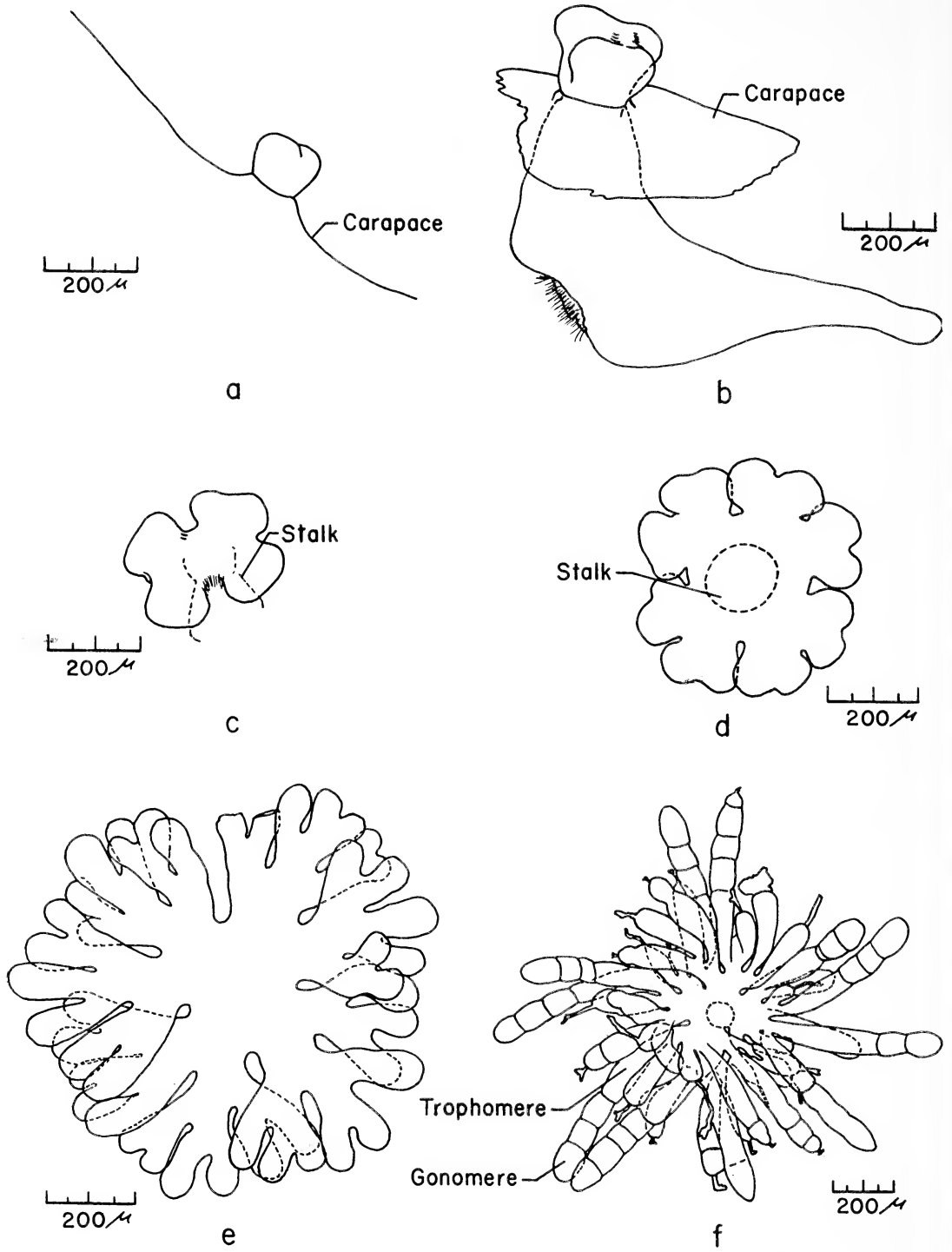


FIG. 4. Drawings illustrating the developmental stages of *Thalassomyces fagei*.

usual frequency or that the parasite interferes with the regulation of molting. In the former case, the external development of *T. fagei* during the intermolt would of necessity be extremely rapid. If the latter is true, as is the case with the rhizocephalans, molting would be held in abeyance while the external development and assumed reproduction of *T. fagei* take place.

In order to resolve this question and others, work on the internal development needs to be undertaken. Most studies on ellobiopsids, including this one, have dealt with the external aspects of these parasites only, while in reality it is the internal aspects which will reveal their biological status.

The observations on the effect of *Thalassomyces fagei* on *Thysanoessa raschii* agree with the reports of Einarsson (1945) on the effects of *T. fagei* on *Thysanoessa inermis*. Einarsson stated that *T. fagei* probably castrates the animal it attacks. None of the parasitized *Thysanoessa raschii* examined in this study had either the male antennal armature or the first pleopods developed as copulatory organs; in the case of females no sign of a thelycum was evident. Einarsson (1945) showed that parasitized mature females had completely disorganized ovaries through which ramifications of the stalk of the parasite extended.

Boschma (1949) sectioned parasitized euphausiids and found that the ellobiopsid did not disorganize the host's ovary, although the protoplasmic excrescences which protrude through holes in the sieve plate extended throughout the organ. The ovary was not degenerated, although Boschma found that all the eggs present were small.

The most complete works on the genus *Thalassomyces* are those by Boschma (1949 and 1959), which contain a comprehensive review of the literature as well as descriptions of the species.

On the basis of these and other observations concerning the biology of ellobiopsids, a number of conclusions and hypotheses can be drawn concerning members of the genus *Thalassomyces*.

1. The development of the structures external to the euphausid and the similarity of these to reproductive structures of *Ellobiopsis* strongly

suggest that they are primarily reproductive. These external structures follow the establishment of a large internal body thought to be of a vegetative nature. The length of "life" of the internal portion of the parasite and its seasonal presence are unknown. Therefore the true percentage infection cannot be determined on the basis of the external structures alone.

2. The external reproductive structures of *T. fagei* appear in early summer in Alaska, whereas they appear in midsummer in the Atlantic. The duration of this manifestation of individual ellobiopsids is unknown.

3. Our observations in this study and those of Einarsson and Boschma on the sexual development of euphausiids support the interpretation that *T. fagei* suppresses the sexual development of the host. Also the ellobiopsid may interfere with the endocrine control of molting, at least during its period of external development.

4. Further understanding of the biological effects of these parasites on planktonic crustaceans will be achieved only by laboratory investigations on the internal development of the parasite and on the nature and fate of the bodies produced in the gonomere.

Thalassomyces sp.

Six specimens of *Thalassomyces* sp. were found to parasitize the mysid *Acanthomysis pseudomacropsis*. The ellobiopsid is generally located on the dorsal surface of the carapace of the mysid. In each case the mysid was parasitized by two ellobiopsids. In one instance, one of the ellobiopsids was located on the carapace, and the other was on the dorsal surface of the sixth abdominal segment of the mysid. The mature *Thalassomyces* specimens were taken in plankton samples from stations in the Kachemak Bay area of Alaska (59°27'N, 151°33'W) in October and December, 1963 and in February, 1964.

The mature parasite has 7–20 short-stalked trophomeres which are ramifications of the single central stalk. The trophomeres average 0.75 mm long, although this feature is variable. The usual number of gonomeres present on each trophomere is three, and no more than this num-

ber have been observed. The transverse diameter of the gonomeres ranges from 0.14 to 0.21 mm, the average being 0.17 mm.

The species identification of these specimens has not been determined. This ellobiopsid may be *T. fagei*, although there are differences in a number of external features of *Thalassomyces* sp. from the specimens of *T. fagei* parasitic on the euphausiid *Thysanoessa raschii* taken in the same area. The number of trophomeres, the length of the trophomere stalk, and the number of gonomeres vary from the previously mentioned species. Boschma (1959) pointed out that a number of variations of this type occur among *T. fagei* individuals parasitic on different species of euphausiids. The location of the ellobiopsid on the carapace tends to support the hypothesis that this is *T. fagei*, while the fact that this species parasitizes a mysid rather than a euphausiid may be sufficient to propose this as a new species, inasmuch as *T. fagei* has only euphausiid hosts. The only *Thalassomyces* species reported to parasitize a mysid is *T. fasciatus*. This ellobiopsid is located on the ventral side of the first abdominal segment of its host.

Until more material is available and can be examined by an authority, it is advisable to consider this ellobiopsid as *Thalassomyces* sp.

Thalassomyces capillosus

The first report of ellobiopsids from the northern and eastern Pacific was that of McCauley (1962). He found *Thalassomyces capillosus* (Fage), formerly known as *Amallocystis capillosus*, on a specimen of *Pasiphaea pacifica* Rathbun, a pelagic shrimp taken 15 miles west of Coos Bay, Oregon (43°20.4'N, 124°45.8' W) in a midwater trawl. McCauley (1962) stated, "This work adds *P. pacifica* as a host and extends the known range of this parasite to the north-eastern Pacific." According to McCauley, *T. capillosus* had previously been described as parasitic on several species of pasiphaeid shrimp, most of which were taken in the north Atlantic.

Five *Pasiphaea pacifica* taken by the Exploratory Fishing and Gear Research Base of the Bureau of Commercial Fisheries, Juneau, Alaska, were examined for ellobiopsids. A single speci-

men of *P. pacifica* taken by a shrimp trawl at station No. 427 located in Orca Bay, Prince William Sound, Alaska (60°34'N, 146°01'W) was parasitized. This individual was taken between depths of 74 and 120 fathoms on September 9, 1962, by Rathjen (1963). In addition, a single specimen taken in Lynn Canal in southeastern Alaska (58°51.2' N, 135°15.5'W) was parasitized by *T. capillosus*. This pasiphaeid was taken May 14, 1964, by an Isaac-Kidd midwater trawl at a depth of 59.6 fathoms.

The ellobiopsid is located dorsal to the eyes of the host at the base of the rostrum. On one specimen there were approximately 40–50 trophomeres on either side of the rostrum; on the other specimen there were 50–60. This estimation of the number of trophomeres on the first may not be accurate because the specimen was in poor condition. Distal to the trophomere of the parasite is one or, more commonly, two gonomeres. The terminal gonomere is ovoid, almost twice as long as broad. When two gonomeres are present, the proximal one is somewhat rectangular because of the septa which separate it from the more distal gonomere and from the trophomere.

The morphology of the parasite, its size and location on the host, and the host species agree for the most part with the description of *T. capillosus* (Fage). The only discrepancy was that rather than a single gonomere there were almost always two gonomeres on each trophomere.

Effects of *T. capillosus* on the carapace of *P. pacifica* similar to those found by McCauley were noted. The rostrum is distorted and projects almost dorsad rather than anteriad. On either side of the base of the rostrum is a swelling not found in unparasitized *P. pacifica*. A dumbbell-shaped opening in the carapace extends between the two swellings. A tuft of trophomeres of *T. capillosus* extends from the tissue of the host through both of the expanded ends of the slit. Figure 5 is a camera lucida drawing illustrating the rostrum of a parasitized *P. pacifica*.

This study extends the known range of *T. capillosus* as a parasite on *Pasiphaea pacifica* from off the Oregon coast (McCauley, 1962) to the Prince William Sound area of Alaska. It is expected that further observations will fill in the range and possibly extend it still farther.

Ellobiopsis chattoni

The genus *Ellobiopsis* contains two species, *E. fagei* Hovasse and *E. chattoni* Caullery. *E. fagei* was described as parasitic on the copepod *Clausocalanus arcuicornis* Dana by Hovasse (1951). *E. chattoni* is known to be parasitic on the following copepods: *Calanus finmarchicus* (Marshall et al., 1934; Marshall and Orr, 1955; Jepps, 1937); *Calanus belgolandicus* (Boschma, 1949); *Pseudocalanus minutus* (Marshall, 1949); and *Acartia clausii* (Boschma, 1956). Marshall et al. and Marshall and Orr state that *E. chattoni* is more common on *Calanus* during the summer than the winter.

In our investigation *Metridia longa* was found to be a host for *Ellobiopsis chattoni*. This is the first record of a species of *Metridia* as host for ellobiopsids. *M. lucens*, which was present in the same samples, was not found to be parasitized by *E. chattoni*. Parasites were observed only on Stage V males and females. *M. longa* was the only copepod taken which was host to a species of ellobiopsid.

The plankton samples examined during this study were taken in southeastern Alaska at the mouth of Auke Bay (58°21'N, 134°41'W) by the Oceanography Investigation of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. The samples were taken monthly during 1962 and 1963. Samples were taken both during the day and at night. *Metridia longa* and *M. lucens* were the most abundant copepods in the Auke Bay samples taken during

the late fall in both 1962 and 1963. Throughout the other seasons *Metridia* are taken in considerably fewer numbers. At night both species of *Metridia* are common in the sample taken just beneath the surface, whereas in the daytime *Metridia* are most common in the samples taken from approximately 20 m. Few *Metridia* were taken in the samples from Kasitsna Bay, Alaska, and none of these were parasitized by *E. chattoni*.

E. chattoni was most abundant in the samples from Auke Bay taken in October and November of 1962 and 1963. The percentage of infection was established by examining 250 specimens of *Metridia* and calculating the percentage of infection in this subsample. Samples taken in the middle of November, 1962 showed the highest infection rate. The percentage of infected copepods ranged from 7.7% in the daytime samples to 22.4% in the nighttime samples taken at the same station. No explanation of this difference is available. During October and November, 1963 approximately 5% of the *Metridia* specimens were found to be parasitized by *E. chattoni*.

The morphology and development of *E. chattoni* is described and discussed by Jepps (1937). Our observations of *E. chattoni* on *Metridia* agree with those reported by Jepps on its parasitizing *Calanus finmarchicus*. An ellobiopsid individual initially appears as a small knoblike structure on one of the setae of any of the cephalic appendages. The mature individuals are attached by a stalk which extends into the tissue of the host's appendage. There are one or two gonomeres present on the mature ellobiopsid. The distal gonomere sometimes has an "apical cone" as described by Jepps. Although several immature *E. chattoni* may be located on a single host, no more than three mature parasites were observed on any single specimen of *M. longa*.

The finding of *Ellobiopsis chattoni* on *Metridia longa* in the coastal waters of southeastern Alaska extends the known range of this parasite from the northern Atlantic Ocean to the north-eastern Pacific Ocean. This is the first report of *E. chattoni* taken in the Pacific.

ACKNOWLEDGMENTS

The authors would like to thank the following individuals whose work has aided this study:

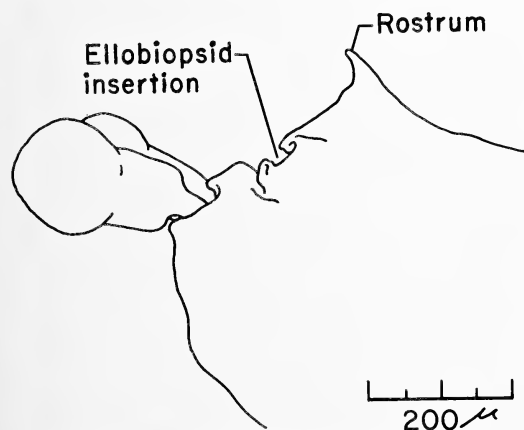


FIG. 5. Drawing showing the anterior portion of the carapace of an infected *Pasiphaea pacifica*.

Mr. Roland McBride, who maintains the Bureau of Commercial Fisheries Kasitsna Bay Shellfish Laboratory and is in charge of carrying out the year-round plankton sampling program; Mr. Jerrold Olson, who took the photographs; Mr. Gerald Reid, project leader for the zooplankton investigation being carried out in Auke Bay, and who allowed the use of the plankton samples taken in that area; and Miss Gail Heron and Mr. Dave Damkaer of the University of Washington Department of Oceanography, who verified the identification of the copepods.

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Four New Diclidophorids (Monogenoidea) Parasitic on the Gills of Marine Fishes from the Southwest Coast of India

R. VISWANATHAN UNNITHAN¹

DURING THE COURSE OF STUDIES on the parasites of marine food fishes from the Indian seas, in the Marine Biological Laboratory at Trivandrum and the Central Marine Fisheries Research Institute at Mandapam Camp, the author collected four new species of monogenetic trematodes belonging to the family Diclidophoridae Fuhrmann, 1928. These species are described below. The collection and treatment of specimens was as described in a previous work (Unnithan, 1957:28-29).

Family DICLIDOPHORIDAE Fuhrmann, 1928,
sensu Price, 1943

Subfamily DICLIDOPHORINAE Cerf., 1896,
sensu emend Price, 1943

Upenicola n. gen.

GENERIC DIAGNOSIS: Diclidophorinae with a mazocraeid body shape; haptor constricted posteriorly, without extension of internal organs except the unbranched terminal ends of the crura; clamps, like sucker frames, with heavy cuticularization; clamp skeleton, though it resembles *Diclidophora*, is much different; no muscular incipient sucker present in the clamp; lappet absent; prepharynx present; male genital pore armed with six hooks; cirrus and penis absent; testes intercrural, postovarian; vitellaria large; ovary median, bent, club shaped, vaginal duct present; vitelline ducts absent; huge pasprostata present. Parasitic on the gills of marine fishes.

GENOTYPE: *Upenicola upeneoides* n. sp.

Upenicola upeneoides n. sp.

Figs. 1-5

Body elongate oval, anterior fourth tapering with rounded tip, posterior fourth formed by the haptor, haptor demarcated from the rest of the body by a shallow constriction on each side,

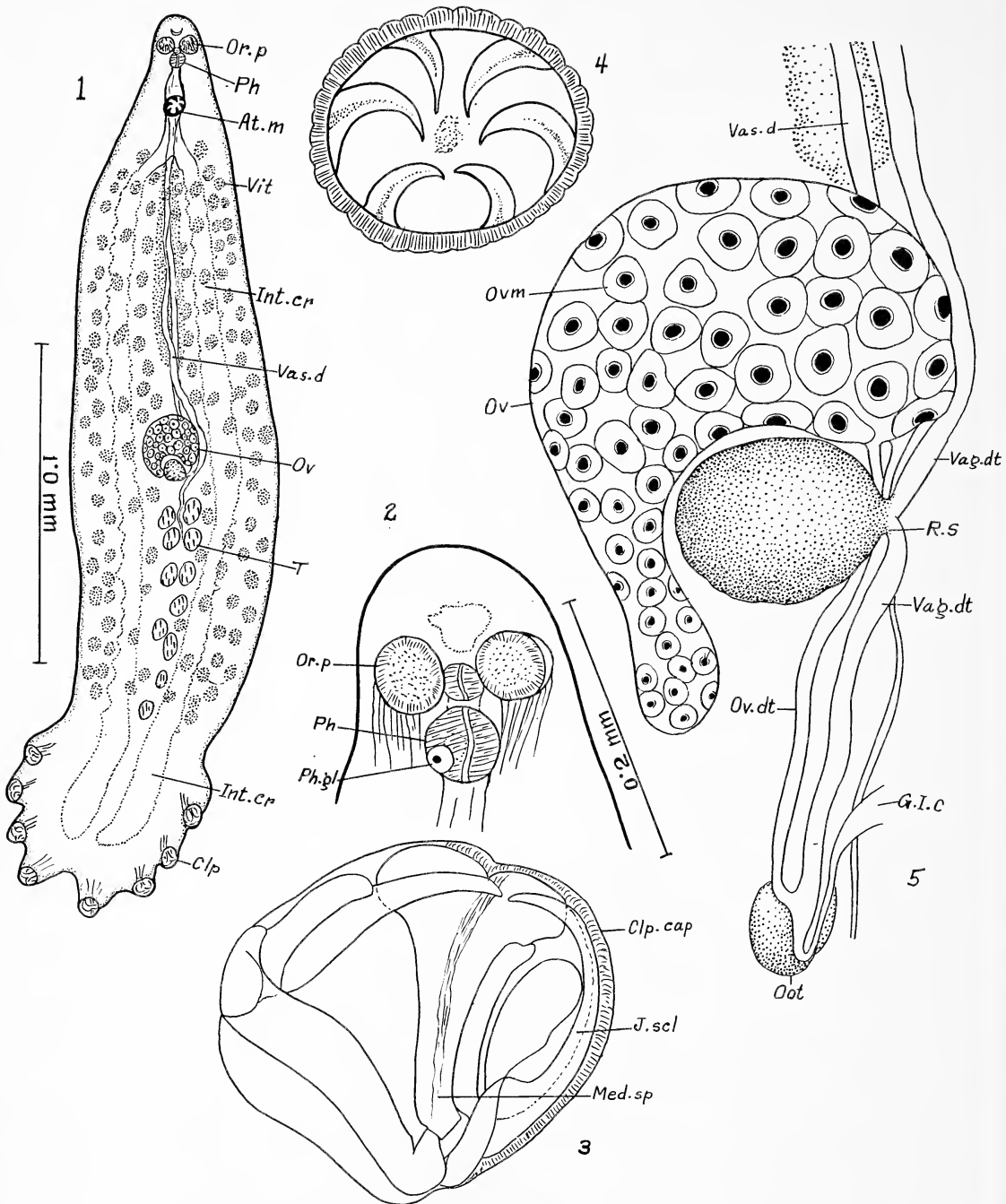
haptor with a prominent posterior median notch and three shallow lateral notches on each side (Fig. 1). Total length 2.9 mm; maximum width across middle of the body, 63 μ .

Mouth subterminal and crescentic; oral pouches spherical with a thick muscular rim, right pouch 63 μ and left pouch 58 μ in diameter; prepharynx small, spherical, 21 μ wide, situated between the oral pouches; pharynx fairly large, spherical (Fig. 2), anterior border slightly overlapping the prepharynx. From the oral pouches and the pharynx short thin parallel muscle fibers run backward to the level of the male pore. Oesophagus wide but ill-defined and unbranched, bifurcates into the intestinal crura about 535 μ from the anterior end of the body. The crura are wide and extend into the haptor where they end blindly close to one another; distal ends of the crura slightly enlarged, the outer branches of each crus simple short and wide, intercrural branches short and ill-defined except in the testes zone; crura in the haptoral region devoid of lateral branches; crura and their branches obscured by the large overlying vitelline follicle.

Haptor mazocraeid in shape, almost as wide as body with four clamps on each side of the posterior median notch, each clamp situated in the apex between the two adjoining notches, spherical or ovoid, 63 \times 63 μ -63 \times 84 μ , right and left clamp symmetrical, sessile; clamp capsule devoid of oblique striae, lip of the capsule narrow and thin; clamp sclerites (Fig. 3) more or less declidophorid in structure but shape slightly different, cuticularization is greater and the fleshy structure noticeable in diclidophorid clamps absent, distal end of the median spring highly expanded; terminal median lappet absent.

Testes 11, arranged in two unequal longitudinal rows, 7 in the right and 4 in the left row, postovarian and intercrural, rectangular or oval 63 \times 21 μ -63 \times 84 μ ; vas deferens thin and narrow, originates from the anterior region

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FIGS. 1-5. *Upenicola upeneoides* n. gen., n. sp. 1, Complete worm, dorsal view; 2, anterior region, dorsal view; 3, second anterior clamp of the right side, dorsal view; 4, male genital pore showing the armature, ventral view; 5, ovarian region, dorsal view.

of the testes and passing beneath the ovary opens into the male genital pore. In front of the ovary it is surrounded by a large pasprostata 631 μ long and 168 μ wide, which extends to the angle of the intestinal bifurcation. Male genital pore situated 294 μ from the anterior end of the body, is ventral circular, with a thin rim and armed with six conical, curved spines (Fig. 4). Penis and cirrus not observed.

Ovary simple, somewhat club-shaped, with a large distal portion, $210 \times 189 \mu$ (Fig. 5) and situated in front of the testes zone, curving round the median seminal receptacle; ova of different sizes, largest ones being present at the distal end; oviduct thin and narrow, originates from the posterior corner of the distal part of the ovary, runs backward parallel to the male genital duct, and opens into a spherical dilatation, probably the ootype. Uterus not very clear. Egg not observed.

Vitellaria present along the lateral field from the level of the intestinal bifurcation to the junction between the ovary and the haptor, not confluent posteriorly; follicles not very numerous but large, spherical or polygonal, 63–82 μ wide. Transverse and median vitelline ducts not very distinct.

Vagina absent (?), but a vaginal duct is traced arising from the spherical deeply stained region (ootype) close to the terminal end of the oviduct and emptying into the huge receptaculum seminis. This duct is filled with a dark substance, probably a mixture of foreign sperms and vitelline matter. Receptaculum seminis irregularly oval $105 \times 84 \mu$, accommodated almost within the curve of the ovary. From the receptaculum seminis the vaginal duct can be traced as a more median, narrow duct up to the anterior level of the ovarian zone beyond which it is indistinct; this duct also is filled with dark matter as in the previous duct.

HOST: *Upeneus vittatus* (Forskål), on the gills.

LOCALITY: Trivandrum (southwest coast of India). One specimen collected 19 April 1956.

DISCUSSION

The genus *Upenicola* closely resembles *Diclidophora* Diesing, 1850, in the shape of the body,

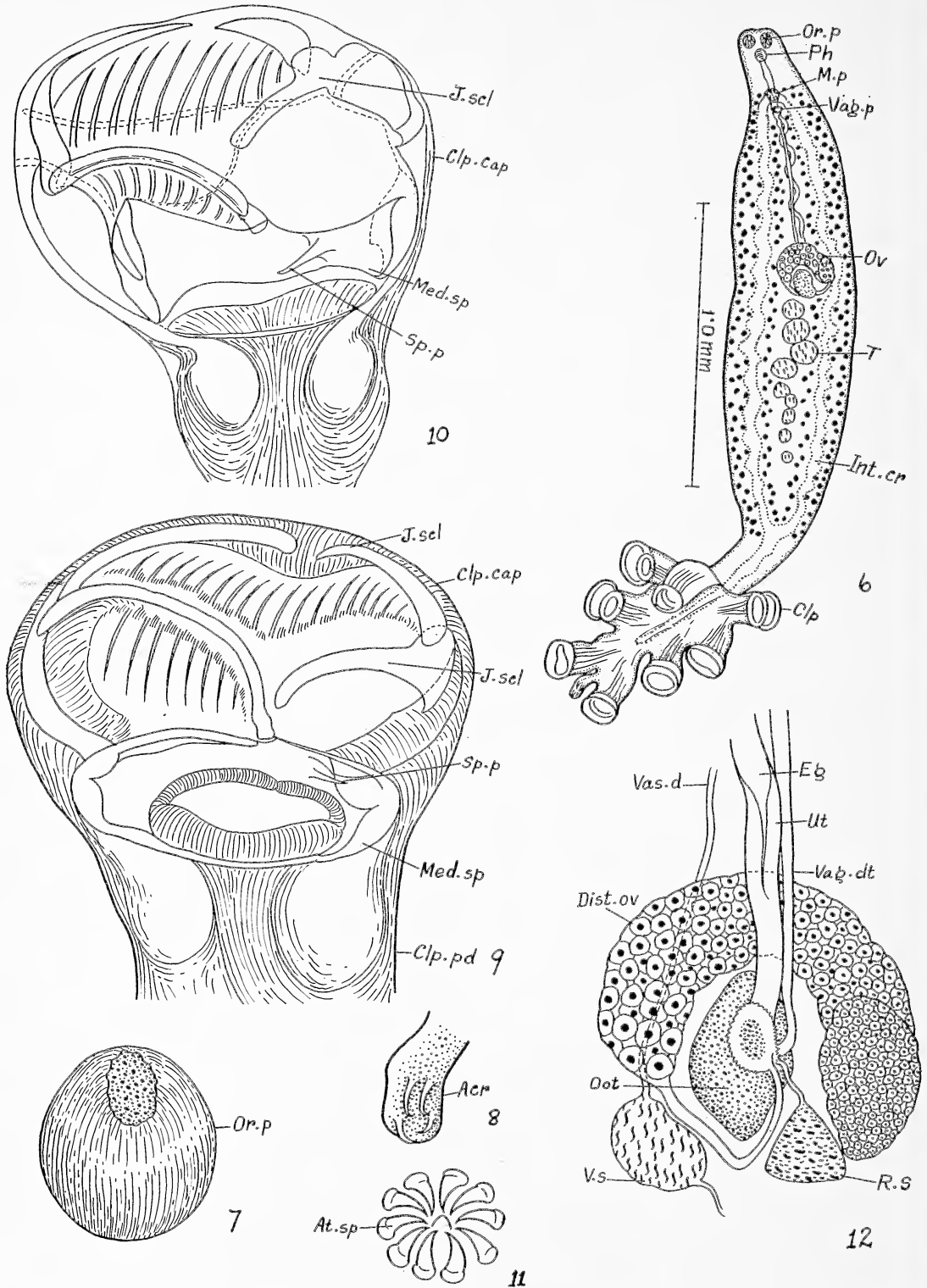
structure of the clamps, absence of vagina, structure of the male genital pore, etc. But in *Upenicola* the haptor is clearly demarcated from the body and the clamps are sessile, with greater cuticularization of sclerites, and the fleshy structures of Diclidophorids are absent. Though a vaginal pore is apparently absent it is presumed that a temporary slitlike opening may be present for the outlet of the contents in the vaginal duct, which is so well formed. This aperture may be formed at the terminus of the vaginal duct at the time of sperm transference. The distribution of the testes is unique in this monogenoidean. In *Diclidophora* there are numerous testes, which occupy both intercrural and extracrural regions, and some posterior ones may also extend into the haptor. But in this species the number is limited to 11, more or less, and they are confined to the intercrural region between the ovary and the haptor. Moreover, there is no penis or cirrus in this species, while a pasprostata is well developed; but in *Diclidophora* a penis or cirrus, as the male intromittent organ, is always present and a pasprostata is absent. Another important difference is that, while in *Diclidophora* the male intromittent organ is armed with numerous spines, in the present species the male pore carries only six curved spines. Also the vitelline follicles are larger and fewer, and a prepharynx is present.

These marked differences make it necessary to create the new genus *Upenicola* to accommodate the new species.

The generic name signifies that the gill trematode inhabits *Upeneus* spp. of fishes, and the specific name is the name of the host.

Subfamily CHORICOTYLINAE Sproston, 1946 *Urocotyle* n. gen.

GENERIC DIAGNOSIS: Choricotylinae, with a short stem separating the haptor from the body proper; clamps pedunculate, choricotylid, with more advancement; median spring in the form of a ring at the base of the clamp and with the ventral half broader, platelike, with long cuticularized peglike spine arising from it; riblike cuticularized thickenings present; abaxial and adaxial half asymmetrical; with tail-like anchored lappet; male genital pore armed; vagina present, unarmed, behind the male genital pore;



FIGS. 6-12. *Urocotyle pristipoma* n. gen., n. sp. 6, Complete worm, ventral view; 7, oral pouch; 8, terminal lappet with anchors; 9, distalmost clamp of the left side, dorsal view; 10, distal second clamp of the left side, ventral view; 11, armature of the male genital pore, ventral view; 12, ovarian region, dorsal view.

oral pouches "saccular"; ovary C-shaped, testes postovarian; vitellaria large; receptaculum seminis and seminal vesicle present. Parasitic on the gills of marine fishes.

GENOTYPE: *Urocotyle pristipoma* n. sp.

Urocotyle pristipoma n. sp.

Figs. 6–12

Body spindle-shaped, connected by a short narrow isthmus with a haptor (Fig. 6). Total length 2.83 mm and maximum width 0.429 mm across the middle of the body proper.

Mouth subterminal, slitlike, transversely elongate and situated immediately in front of the anterior border of the oral pouches. Oral pouches (Fig. 7) almost spherical or vesicular, $52 \times 42 \mu$, with a narrow oval aperture which is plugged with a dark substance; wall of the pouch thick, muscular, and fibrous. (It is interesting to note that the oral pouches of this species are slightly more advanced than are those of Microcotylidae and Gastrocotylidae, showing a remote resemblance to a sucker-like structure embedded in the body muscle, and are devoid of the long and wavy muscle bundles which are usually found attached to the oral pouches of many species of Microcotylidae and Gastrocotylidae.) Pharynx median, oval, thin-walled, more or less the same size as the oral pouches, $52 \times 40 \mu$. Oesophagus short, narrow, and without branches, bifurcating into the two crura at the level of the male genital pore, 0.185 mm from the anterior end; crura fairly wide, with irregular lateral pouchlike bulgings. In front of the narrow isthmus between the body and haptor the two crura become confluent across the median line, and the resulting single median unbranched crus extends through the isthmus as a tapering tube into the haptor about two-thirds its total length (Fig. 6).

Haptor one-fourth the total length, with four pairs of symmetrical clamps and a median posterior tail-like lappet. Lappet cylindrical, $147 \times 42 \mu$, and armed with double pair of anchors, of which the anterior pair is prominently hooked and measures 12μ in length, while the posterior pair is shorter (8μ long) and only slightly curved. Clamps with stout cylindrical muscular peduncles; clamp capsule thick and fleshy with

broad fleshy lips. Each clamp with a broad, well-developed, cuticularized sclerite at the base, the lateral ends of which arch upwards as a flap on each side, the adjacent posterior margins being connected dorsally by a thin, narrow, cuticularized bridge, the entire structure thus forming an uneven ring. This structure represents the median spring. From the inner surface of this broad ventral platelike sclerite a long and narrow peglike, heavily cuticularized spine projects into the clamp capsule. The rest of the clamp armature resembles more or less that of *Choricotyle* except that here it appears to be more advanced in structure. It consists of a pair of oblique sclerites, one long and narrow, the other short and broad; the inner end of the shorter is articulated with the inner end of the longer, which in turn is attached to a small concavity on the anterior margin of the median ring sclerite. There is a second pair of unequal sclerites with slightly curved inner ends along the margin of the clamp capsule. Behind this is a third pair consisting of one long and narrow component, another broad and short component. Both of these articulate with the lateral sides of the median spring. The wall of the clamp capsule has numerous cuticularized ridgelike thickenings.

Testes oval or spherical, $63\text{--}105 \mu$ wide, nine in number, and distributed in a longitudinal, alternating intercrural row between the ovary and the intestinal confluence. Seminal vesicle irregularly oval, $60 \times 48 \mu$, situated close to the anteriormost testis and with small vasa efferentia directed towards the testes. Vas deferens long and narrow, arises from the anterior margin of the seminal vesicle and extends forward ventrally to the left half of the ovary. Beyond this level it extends as a wavy duct parallel to the vaginal duct on its right side, and opens out through the male pore by way of the unarmed conical muscular penis. Male genital pore situated at the angle of intestinal bifurcation and 0.185 mm from the anterior end. It is a small ventral aperture with an irregular rim, armed with a circlet of 10 sickle-shaped short hooks (Fig. 11), which converge to the center of the pore.

Ovary median, C-shaped, situated in front of

the testes zone, with a proximal right end expanded into an oval mass representing the proximal ovary (Fig. 12). Ova are large in the distal part of the ovary. Oviduct arises from the distal end of the ovary, proceeds backward parallel to the left posterior margin of the ootype and opens into the latter at its base by the right side. Uterus wide with semicuticularized walls, arises from the anterior margin of the ootype, extends forward median ventrally and opens out by the uterine pore situated immediately in front of the male genital pore. Egg well formed, spindle-shaped, $80 \times 36 \mu$, but with anterior filament broken, observed in the mid-ovarian zone.

Vitellaria coextensive with the crura and their branches from the level of intestinal bifurcation to the proximal level of the isthmus between the haptor and body. At this level vitellaria become confluent across the median line along with the intestinal confluence; vitelline follicles comparatively large, spherical or polygonal, 24–36 μ wide, few in number. Median and transverse vitelline ducts not observed.

Ootype median, spindle-shaped, $120 \times 80 \mu$, situated between the loops of the ovary and covered by slightly elongated cells except for a central "white" space, where the various genital ducts meet (Fig. 12). Genito-intestinal canal arises from this space and opens into the right intestinal crus.

Vagina median dorsal, unarmed, of the same size as the male genital pore and situated in the angle of the intestinal bifurcation (Fig. 6). Vaginal duct median dorsal, crosses the ovarian zone and opens into the central wide space of the ootype; seminal receptacle triangular, 40 μ long, and placed between the proximal ovary and ootype close to the testes zone. A short narrow duct from the seminal receptacle opens into the ootype close to the entrance of the vaginal duct.

HOST: *Pristipoma guoraca* Blkr., on the gills.

LOCALITY: Trivandrum (southwest coast of India). One specimen collected 20 August 1955.

DISCUSSION

The genus *Urocotyle* is allied to *Choricotyle* Van Benden and Hesse, 1863, but differs markedly in the clamp structure. The platelike

cuticularization of the median spring and its advancement as a cuticularized rim in *Urocotyle* is by far too important a character to be regarded as a variation. It is of definite significance in the evolution of the group. Moreover, the presence of a peglike spine on this cuticularized plate sufficiently warrants according this monogeneoid a new status. The short isthmus separating or connecting the body with the haptor of *Urocotyle* is not observed in any existing species of *Choricotyle*. The number of spines around the male genital pore may be of significance only in species, but the presence or absence of a definite vagina is of greater significance. In species of *Choricotyle* there is no vagina, while in those of *Urocotyle* a median dorsal unarmed vagina is present. In view of these marked differences *Urocotyle* is created as a new genus, with *Urocotyle pristipoma* n. sp. as the type species.

The generic name refers to the haptor with a tail, i.e., the lappet. The specific name refers to the host.

Dussumericola n. gen.

GENERIC DIAGNOSIS: Choricotylinae, with haptor demarcated from body by deep lateral constrictions. Clamps with long peduncles, median spring of the clamp broad and ringlike, with long spinous process; anchors and lappet absent; mouth with a sphincter-like ridge; pharynx larger than oral pouches; crura confluent with a median crus in the haptor; testes few, intercrural, post ovarian but not entering haptor; male genital pore in the mid-oesophageal region, armed with a ring of 10 curved hooks; ovary U-shaped; median vitelline duct very large; receptaculum seminis present; vagina unarmed, median dorsal at the intestinal bifurcation; vaginal duct joins the ootype through the receptaculum seminis; genito-intestinal canal arises from receptaculum seminis. Parasitic on dussumerid fishes.

GENOTYPE: *Dussumericola dussumeria* n. sp.

Dussumericola dussumeria n. sp.

Figs. 13–16

Body divisible into an anterior narrow neck, a median oval body, and a posterior expanded haptor formed of two winglike halves, the haptor being demarcated from the body by deep

lateral notches (Fig. 13). Total length 3.7–3.9 mm; maximum width across the ovarian zone, 0.9 mm.

Mouth subterminal, circular, bordered by a 'sphincter' of thin muscle fibers; oral pouches thin-walled, elliptical or oval, $16 \times 12 \mu$ – $20 \times 16 \mu$, situated behind the mouth and parallel to the median line; pharynx median, oval, $36 \times 28 \mu$, and with a row of gland cells on each dorso-lateral side. Pharynx and oral pouches have long muscle fibers extending to the level of the male genital pore. Oesophagus wide, without lateral branches and bifurcating into the crura at the level of the vagina 0.609 mm from the anterior end of the body; crura wide and saclike with irregular margin. At the junction of the body and the haptor the two crura become confluent and continue into the haptor as a single median crus which considerably expands in the base of the haptor. From the sides of this median crus are given off short stumpy branches to the bases of each peduncle. The intercrural field is reduced in front of and behind the ovarian zone owing to the highly expanded condition of the crura (Fig. 13).

Haptor forms slightly less than half the total length, with four pairs of pedunculate clamps; peduncles of varying length, each with a thick bundle of axial muscle fibers extending from the base of the clamp to the middle of the haptor; clamps triangular with rounded corners, $189 \times 189 \mu$ – $210 \times 210 \mu$, with fleshy capsule and thick lips but no riblike striae in the wall of the capsule. Clamp structure (Fig. 14) more or less as in *Urocotyle pristipoma*; but the lidlike median spring forms a broader cuticularized continuous ring at the base of the clamp, the spinous process is longer and narrower, paired sclerites on either side are long and narrow, and the clamp capsule contains two fleshy suckerlike pads, one at the base and another in the distal dorsal region of the clamp. Terminal lappet and anchors absent.

Testes five to six, spherical, 42μ in diameter, and confined to a small intercrural space behind the ovary, not entering the haptor. Vas deferens long and narrow, arises from the anterior margin of the testes, runs forward along the median line and, crossing over to the left side of the vagina, opens into the base of the penis; penis

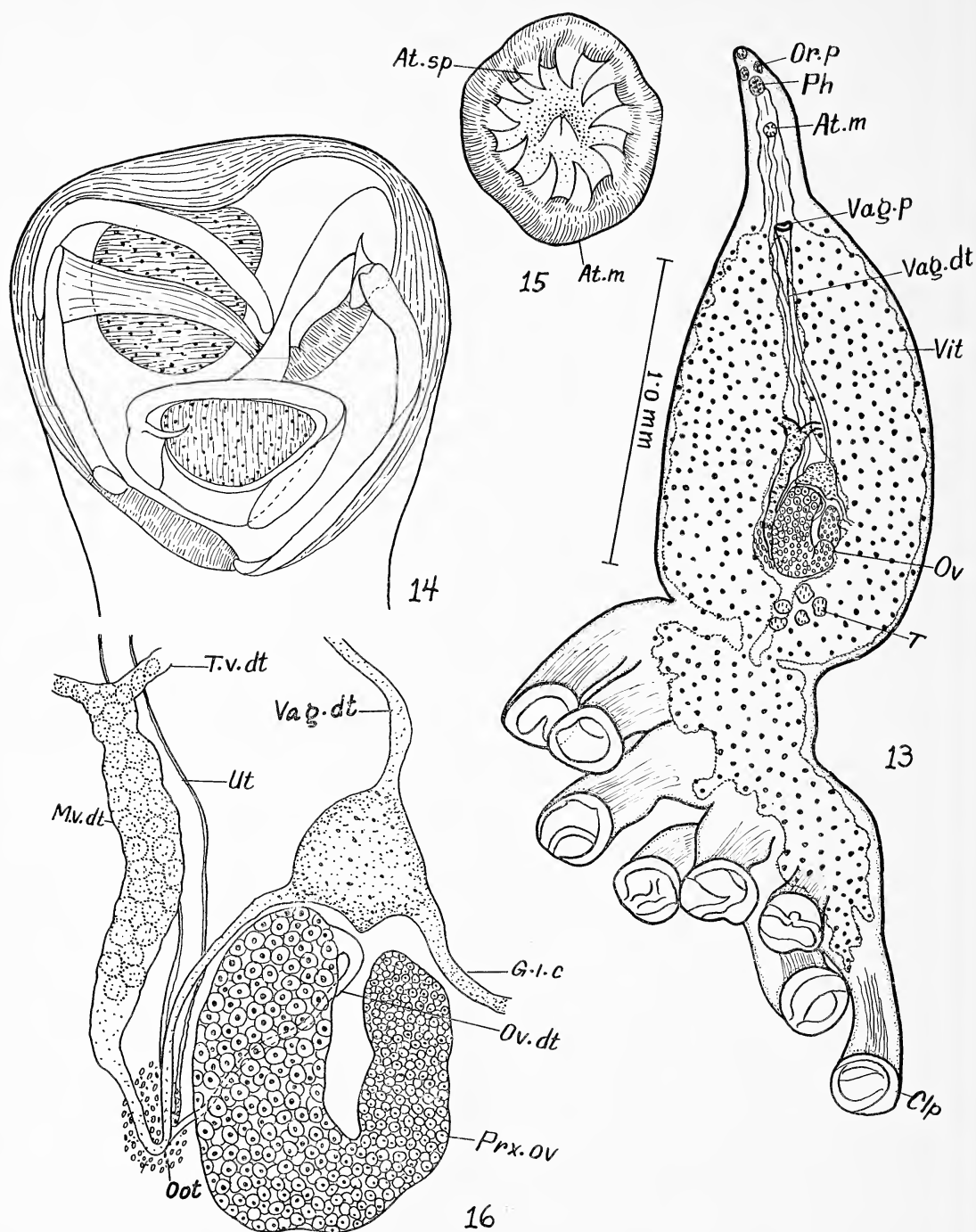
muscular, conical, unarmed; male genital pore median ventral armed with a ring of 10 conical convergent cuticularized spines (Fig. 15) and situated midway between the mouth and intestinal bifurcation. Seminal vesicle and penis bulb absent.

Ovary U-shaped, $273 \times 210 \mu$, and situated in the median intercrural field in front of the testes; proximal limb narrower and shorter with small ova, distal limb with large ova (Fig. 16); oviduct arises from the distal end of the ovary and curving downward runs obliquely beneath the ovary to open into the ootype close to the median vitelline duct; uterus long and narrow, arises from the anterior margin of the ootype and runs forward along the median ventral plane, where it can be traced up to the level of intestinal bifurcation.

Vitellaria coextensive with the crura from the zone of intestinal bifurcation to the terminal end of the median crus in the haptor; follicles spherical or polygonal, 21μ wide; transverse vitelline ducts arise from each side in the middle of the body proper and unite to form a long, wide, median vitelline duct, with large follicles in the anterior two-thirds (Fig. 16). The narrow posterior end of this duct opens into the ootype.

Ootype small, oval, surrounded by two or three rows of small Mehlis' gland cells and situated at the terminal end of the median vitelline duct on the left posterior margin of the ovary.

Vagina, median dorsal (Fig. 13), unarmed, and in the form of a transverse slitlike aperture, situated at the level of the intestinal bifurcation; vaginal duct wide and thick-walled in the anterior half, while narrow and thin-walled in the posterior half. At the level of the transverse vitelline ducts the vaginal canal curves to the right side and opens into the anterior corner of the receptaculum seminis; receptaculum seminis median triangular, $126 \times 126 \mu$, placed close to the anterior margin of the ovarian zone. From the left corner of the receptaculum seminis the vaginal duct continues around the distal limb of the ovary and opens into the ootype close to the oviduct. Genito-intestinal canal arises from the posterior margin of the receptaculum seminis, runs obliquely backward and opens into the right crus.



FIGS. 13-16. *Dussummericola dussummeria* n. gen., n. sp. 13, Complete worm, dorsal view; 14, proximal third clasp, dorsal view; 15, male genital pore showing the armature of hooks; 16, ovarian region, dorsal view.

HOST: *Dussumeria basselti* Blkr., on the gills.

LOCALITY: Trivandrum (southwest coast of India). Two specimens collected 27 November 1954.

DISCUSSION

The genus *Dussumericola* possesses all the characters of the subfamily Choricotylinae, but at the same time it shows a number of unique characters which distinguish it from all the known genera included under the subfamily. It closely resembles *Urocotyle* n. gen. in many characters, especially in the structure of the clamps and the vagina, but differs from it in the shape and proportions of the body and in the absence of a terminal anchored lappet. *Dussumericola* approaches *Diclidophora* Dies. (Subfam. Diclidophorinae) in shape, but differs in the structure of the clamps. Moreover, in *Diclidophora* a vagina is lacking, while it is present in *Dussumericola*. The new genus differs from *Heterobothrium* Cerf., 1895, in the absence of a long isthmus between the body and the haptor and in the presence of a vagina. It closely resembles *Cyclobothrium* Cerf., 1895, and *Choricotyle* Van Benden and Hesse, 1863, in a number of characters, but differs from both in the presence of a vagina. The chief character which distinguishes the new genus from *Diclidophoropsis* Gallien, 1937, is that the latter possesses a double lateral vagina. The resemblance between the present species and *Echinoplema* Raecke, 1945, is more pronounced: in both the haptor is demarcated from the body by a prominent lateral constriction, the clamps have muscular pads, a terminal lappet is absent, a single vagina is present, and the vitellaria extend into the haptor; but in *Echinoplema* the vagina opens laterally, while in this species it is median-dorsal and situated at the level of intestinal bifurcation.

Thus the characters of this species which prevent its inclusion under any of the known genera of the subfamily are: (1) the presence of a wide median vitelline duct, (2) the comparatively large size of vitelline follicles, (3) the position of the testes in a limited space between ovary and haptor, the number of testes also being limited, and (4) the position of the single median vagina at the level of intestinal bifurca-

tion. In view of these combinations of unique characters the new genus *Dussumericola* has been created to accommodate this new species, with *Dussumericola dussumeria* as the type species.

Both the generic and the specific name refer to the host.

Keralina n. gen.

GENERIC DIAGNOSIS: Choricotylinae, with a flowerlike circular haptor, with a complete circle of eight clamps borne on short peduncles; clamps choricotyloid but slightly more advanced in structure, capsule lip glandular; terminal lappet and anchors absent; oral pouches fibrous with muscular rim and a median triangular portion; pharynx with two rows of 'teeth,' with glandular and muscular parts; intestinal crura confluent posteriorly and with a median vesicular extension into the haptor; testes postovarian, penis and cirrus absent, male genital pore situated at the level of intestinal bifurcation and armed with eight converging hooks; vitelline follicles large; vitelline ampulla and genito-intestinal canal present; vagina median dorsal, unarmed, and situated in the angle of intestinal bifurcation; egg spindle-shaped and operculate with a filament at each pole. Parasitic on the gills of marine fishes.

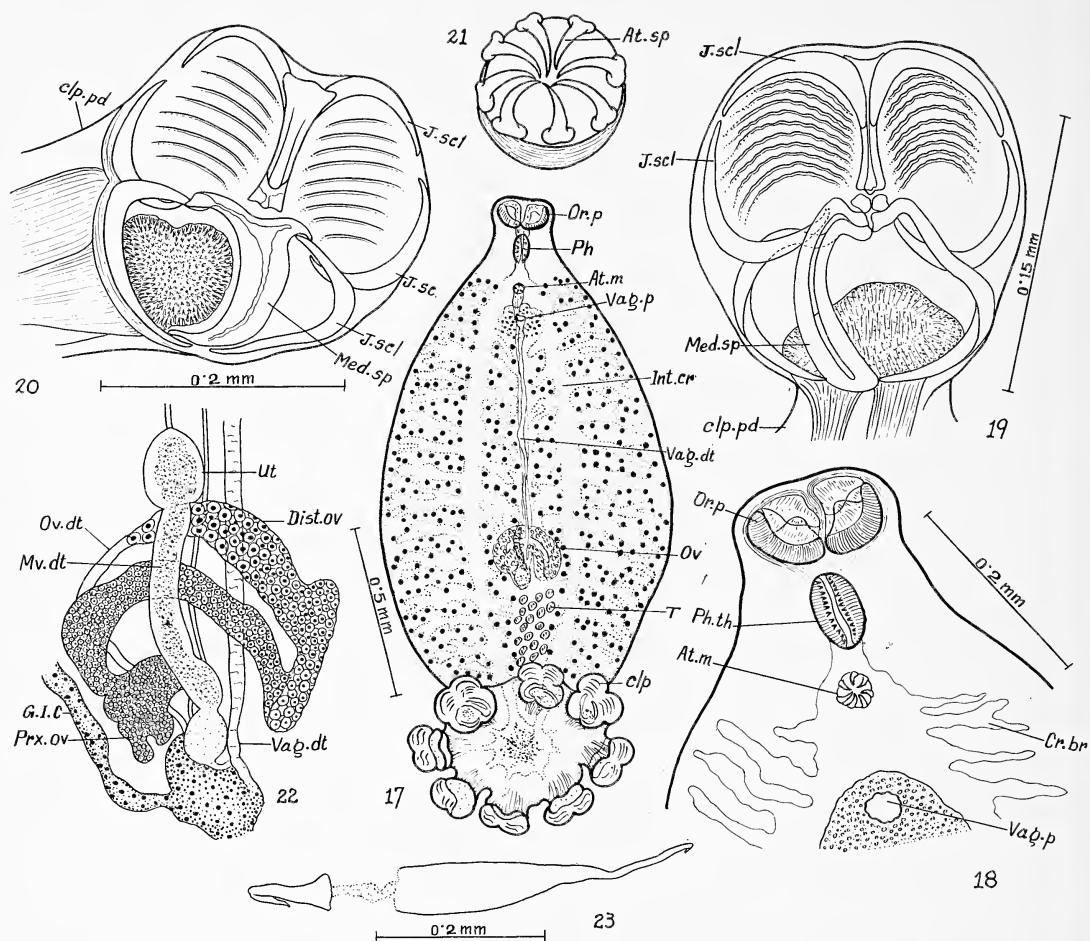
GENOTYPE: *Keralina opisthopterus* n. sp.

Keralina opisthopterus n. sp.

Figs. 17-23

Body broad and more or less oval, with an anterior short neck and a posterior flowerlike, horizontally expanded circular haptor (Fig. 17). Total length 1.15 mm-3.36 mm, and maximum width across middle of body 0.63-1.45 mm; type specimen 1.74 mm long and 0.84 mm broad.

Mouth subterminal, ventral transverse, and bordered by a thick muscular ridge; oral pouches more or less rectangular $63 \times 63 \mu$ - $126 \times 84 \mu$, cuplike, and fibrous, with a triangular muscular or glandular structure projecting from the base of the concavity (Fig. 18). The inner edges of the two oral pouches are parallel and placed close to each other along the median line; the posterior rim is broad and ridgelike with short



FIGS. 17-23. *Keralina opisthopterus* n. gen., n. sp. 17, Complete worm, ventral view; 18, anterior region, dorsal view; 19, clamp, ventral view; 20, another clamp, ventral view; 21, male genital pore showing the armature of recurved spines; 22, ovarian region, ventral view; 23, egg.

muscle fibers extending from it to the postero-lateral region of the pharynx. Pharynx large, thick, muscular, oval, $63 \times 42 \mu$ – $126 \times 63 \mu$ with a longitudinal row of semicircularized teethlike structures on each side projecting into the axial lumen; in one of the specimens the pharynx is divided into an anterior muscular and a posterior glandular portion. The pharynx and oral pouches occupy the greater portion of the neck region (Fig. 18). Oesophagus short and unbranched, bifurcating into the crura in front of the vagina; lumen of the crura at the bifurcation region comparatively large; each crus with very long horizontally parallel outer branches with short secondary branches which

do not anastomose; intercrural branches short and directed obliquely backward but not confluent with those of the opposite side; posteriorly the two crura unite in front of the haptor and the united distal end expands into a vesicular structure from the periphery of which short branches lead to the base of each clamp.

Haptor closely resembling that of *Cyclobothrium* Cerf., but with a complete circlet of clamps; connected in the center to the narrow posterior extremity of the body. Clamps eight in number, squarish or polygonal, $126 \times 147 \mu$ – $210 \times 210 \mu$, and arranged radially along the periphery of the circular haptor; clamp peduncles very short with axial muscles extending

from the base of the clamp to the center of the haptor. Clamp structure (Figs. 19 and 20) more or less that of *Choricotyle elongata* (Goto) Llewellyn, 1941, but in a higher stage of evolution; median spring very broad and distally expanded horizontally so as to provide articulation for the lateral jaw sclerites; distal half of clamp with numerous transverse cuticular thickenings, basal half of the clamp capsule with a large bilobed muscular pad to which are connected the axial fibers of the peduncles, and the lip of the clamp capsule is fleshy and glandular. Terminal lappet and anchors absent.

Testes 19–22, small and spherical, 21–42 μ in diameter, and confined to the small intercaecal area between the ovary and the posterior crural confluence; vas deferens long and narrow, arises from the anterior row of the testes, runs forward ventrally along the median plane and opens into the male genital pore; male genital pore median ventral, situated at the level of intestinal bifurcation and armed with a cirlet of eight small, elongately conical, cuticularized spines converging to the center of the pore (Fig. 21); each spine with a fleshy basal cushion embedded in the circular rim of the pore; penis and cirrus absent.

Ovary median, highly convoluted (Fig. 22), curved at right angles to the long axis of the body, and occupying an area $168 \times 168 \mu$ – $315 \times 210 \mu$ of the intercrural space in front of the testes; proximal ovary slightly lobed on the right side of the median line close to the ootype; oviduct arises from the distal end of the ovary and runs obliquely backward to open into the vitelline ampulla; uterus arises from the anterior end of the vitelline ampulla, proceeds ventrally along the median plane parallel to the vaginal duct, and is traceable up to the mass of gland cells surrounding the vaginal region; egg spindle-shaped and operculate, operculum 21 μ long and 42 μ broad, body $210 \times 63 \mu$, anterior filament 126 μ long, and posterior filament 168 μ long.

Vitellaria coextensive with the crura and its branches from the level of intestinal bifurcation, and terminates slightly in front of the intestinal confluence; follicles large and spherical, 21 μ in diameter, not confluent posteriorly. Transverse

vitelline ducts almost empty; median vitelline duct large and filled with vitelline follicles, in irregular dilatations especially at the anterior end, posteriorly the median vitelline duct opens into the vitelline ampulla; vitelline ampulla small, oval, or spherical and slightly embedded in the anterior margin of the receptaculum seminis, into which it opens.

Ootype apparently absent, but a genito-intestinal canal is present, which arises from the right posterior margin of the receptaculum seminis, runs obliquely forward, and opens into the right intestinal crus (Fig. 22).

Vagina median dorsal and unarmed, situated in the angle of intestinal bifurcation, and surrounded by a cluster of deeply staining small spherical gland cells (Figs. 17 and 18) which almost obliterate the vaginal opening; vaginal duct median dorsal, runs backwards as a straight tube, and opens into the receptaculum seminis; the receptaculum seminis is median, irregularly oval, $84 \times 36 \mu$, and situated close to the posterior margin of the ovary.

HOST: *Opisthopterus turdoore* (Cuv.), on the gills and inner opercular wall.

LOCALITY: Trivandrum (southwest coast of India). Seven specimens, three collected on 22 December 1954, and four on 26 July 1955.

DISCUSSION

The genus *Keralina* closely resembles *Choricotyle* Van Ben. and Hesse, 1863, but differs in the shape of the body disposition of the clamps and in the structure of the clamp sclerites. Moreover, terminal lappet and anchors are absent. Of the various species of *Choricotyle*, the recently recorded American species *Choricotyle aspina-chorda* Hargis, 1955, shows the closest resemblance to *Keralina opisthopterus*. They resemble each other in the shape of the body and the haptor, but differ markedly in the distribution of the testes and ovary. *Keralina* closely resembles *Cyclobothrium* Cerf., 1895, in the arrangement of the clamps, but the par- and pre-ovarian testes of *Cyclobothrium* are absent. Moreover, the size and relative position of the testes, the convoluted condition of the ovary, and the comparatively large size of the receptaculum seminis clearly distinguish the present species from *Cyclo-*

bothrium. Even though the new species possesses some of the characters of *Choricotyle* Van Ben. & Hesse and of *Cyclobothrium* Cerf., it is unique in possessing a vagina and the peculiar structure for the pharynx.

From the measurement of the organs in this species it is evident that the various organ systems may change their shapes, sizes, and even extent of distribution during growth; a short worm, 1.7 mm long, has all its organs relatively smaller than another, 3.36 mm long. In the present collection the type specimen is in the testicular phase and, as such, there are numerous testes and the ovary is very small ($168 \times 168 \mu$), while a paratype 3.36 mm long is in the ovarian phase and the ovary is enlarged ($315 \times 210 \mu$). In the latter specimen the testes are practically absent except for two or four, apparently being spent already in the testes phase. In a few specimens the receptaculum seminis is highly pronounced, while in others it is rather empty. The cuticularized structure and the structure of the oral pouches and pharynx do not vary much in this species, but the clamps increase slightly in size during growth. The most variable organs are the ovary and testes. Much emphasis is to be placed on the changeable nature of these organs and organ systems, lest their differences be treated as definitive, and consequently used in the creation of new species.

The generic name indicates that the parasite is found on the Kerala coast; the specific name refers to the host fish.

SUMMARY

From marine fishes of the Indian seas four new species of monogenetic trematodes belonging to the family Diclidophoridae Fuhrmann, 1928, *sensu* Price, 1943, are recorded and described. They are *Upenicola upenoides*, *Urocotyle pristipoma*, *Dussumericola dussumeria*, and *Keralina opisthopterus*. Each of these species has its own host and new genus. All inhabit local marine fishes belonging to closely related families (percoids and clupeids).

ACKNOWLEDGMENTS

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New Fish Records from Hawaii: *Hime*, *Pikea*, and *Omobranchus*

DONALD W. STRASBURG¹

IN THEIR RECENT *Handbook of Hawaiian Fishes* Gosline and Brock (1960) record 584 species of fish from Hawaii, and point out that many more may be expected when depths greater than 100 ft are sampled extensively. About one new Hawaiian fish has been recorded each year since the Handbook's appearance, with most coming from deep water (Gosline, 1960: 28; Randall, 1961: 58; 1963: 432, 447; Strasburg, 1960: 395). The present paper documents two new Hawaiian records obtained by deep handlining, and confirms the presence of a shallow-water blenny hitherto known only under peculiar circumstances.

Thanks are due Mr. Kuni Sakamoto of Honolulu for donating the handlined specimens, Mr. Joseph Harada of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu for contributing the blenny, Dr. William A. Gosline for the loan of specimens in the University of Hawaii collections, and Mr. Tamotsu Nakata of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu for preparing Figure 1.

FAMILY AULOPIDAE

Figure 1 depicts the first recorded Hawaiian specimen of the Aulopidae, an immature female of *Hime japonicus* (Günther). This fish was taken by bottomfishing with a handline at a depth of 780 ft. It was captured on April 15, 1963 by Mr. Kuni Sakamoto of the M/V "Koun Maru" of Honolulu. The capture site lies between Lanai and Kahoolawe, islands near the center of the main Hawaiian group.

Counts made on this specimen are: D 16, A 10, P 11-11, V 9-9, C 9 + 1 + 9, lateral line scales 43-43, transverse scale rows at level of fourth dorsal ray $3\frac{1}{2} + 1 + 5\frac{1}{2}$, predorsal scales 13, branchiostegal rays 13, and gill rakers on

first arch $4 + 1 + 13$. Measurements (in mm) are: standard length 219, head length 65, snout length 17.5, greatest eye diameter 17.7, greatest depth of body 41.3, least depth of caudal peduncle 16.2, snout to dorsal origin (diagonal) 77, length of dorsal base 64, snout to anal origin (diagonal) 165, length of anal base 23, longest dorsal ray (third) 41, longest pectoral ray (third from top) 39, longest pelvic ray (fourth) 44.5, longest anal ray (third) 20, greatest dimension of adipose fin 6.8, and width of bony interorbital 11.

The teeth are arranged in villiform bands in both jaws and on the vomer and palatines. The outer teeth are shorter than the inner ones. The center of the tongue bears an elongate band of tiny villiform teeth which are too small to be seen by the unaided eye, but which can be easily felt by probing with a finger or a needle. There is a single nostril on each side, guarded anteriorly by a small flap of skin.

The fish was frozen after capture and was thawed and photographed three days later. Its life coloration was as follows, based on a 35-mm transparency and field notes: Upper sides brownish-red, with dark-brown saddles running to the midsides beneath the anterior part of the dorsal fin, the posterior part of the dorsal fin, the adipose fin, and just before the caudal base. Interspaces between these saddles streaked with yellow pigment above lateral line. Lower sides silvery-white, blotched irregularly with vermilion. Throat, breast, and belly white; ventral side of tail and gill membranes lemon. Top of head olive-brown, cheeks silvery with red blotches, snout and opercle olive-brown with red blotches, iris yellow. Dorsal fin gray with round vermilion spots arranged in four irregular diagonal rows, largest spots about size of pupil; anal fin pale lemon; lower lobe of caudal yellow, with upper and lower rays streaked with red; upper lobe of caudal gray, blotched irregularly with lemon and red; pelvics lemon with orange blotches; pectorals hyaline with five vermilion

¹ U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Manuscript received August 12, 1964.

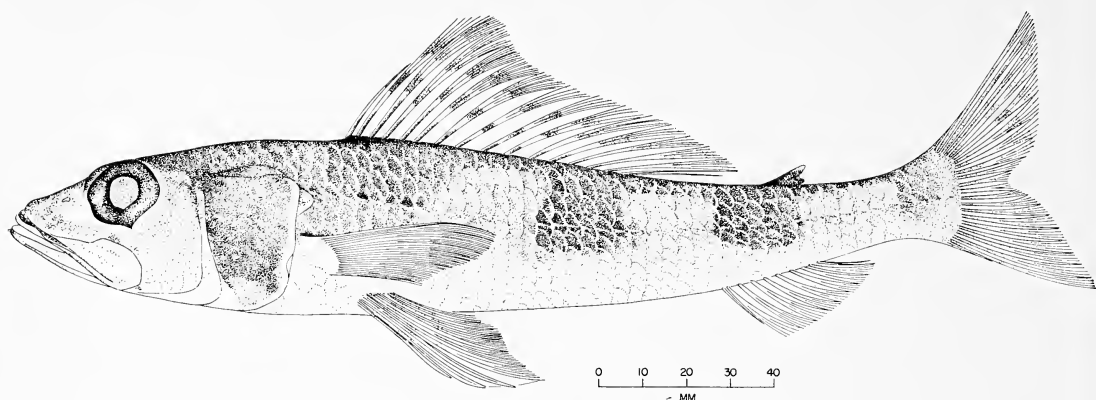


FIG. 1. Hawaiian *Hime japonicus* (Günther), 219 mm in standard length.

bands; adipose fin brown with red distal tip. This coloration agrees with that of the Japanese specimen figured by Kamohara (1955: pl. 9), except that his fish has only weak indications of spotting on the dorsal, caudal, and pectoral fins, and none at all on the cheeks and opercles.

In alcohol the Hawaiian *Hime* is dusky above and pale below. The four dark saddles persist, as does the gray ground color of the dorsal fin and upper caudal lobe. These fins are now white-spotted, for their vermilion pigment has faded completely.

The Hawaiian specimen agrees well with the description of the Japanese type given by Günther (1880:72) and with the brief account of other Japanese material presented by Matsubara (1955:240). *H. japonicus* can be distinguished from its only other congener, *H. damasi* (also from Japan), by its having 15 or 16 dorsal rays, about 43 lateral line scales, and an eye diameter about equal to the snout length, as compared with 14 dorsal rays, about 35 lateral line scales, and the eye diameter shorter than the snout in *damasi*. Among Hawaiian fishes *H. japonicus* superficially resembles the Synodontidae and the Chlorophthalmidae. It can be distinguished from the Synodontidae by its large eye, which is contained 3.6 times in the head length as opposed to 5–6 times in the Synodontidae, and from the Chlorophthalmidae by its long dorsal fin. The dorsal base is 3.5 times the eye diameter in *Hime*, and equals the eye diameter in *Chlorophthalmus*.

The specimen has been deposited in the U. S. National Museum (No. 198224).

FAMILY SERRANIDAE

A second unrecorded Hawaiian fish was taken with the *Hime* discussed above. This was a 214-mm male *Pikea maculata* Döderlein and Steindachner. Another unreported Hawaiian specimen of *P. maculata* was subsequently made available by Dr. Gosline. The latter fish, which is 213 mm in standard length, lacks collection data and its sex cannot be determined. Both specimens are essentially identical with Döderlein and Steindachner's illustration (Steindachner and Döderlein, 1883: pl. 6, fig. 1) of the Japanese type specimen, which is reproduced here as Figure 2.

Counts are the same for both specimens except for pectoral rays and scales. Both fish have D VIII, 12; A III, 8; VI, 5; C 17; branchiostegal rays 7; and gill rakers on the first arch 1 + 1 + 6 (there are also five flat patches of tiny denticles dorsad to the first raker and about four such patches ventrad to the last raker). The 214-mm fish has 68 pore-bearing scales in the lateral line, the 213-mm individual has 64. The 214-mm fish has $6\frac{1}{2} + 1 + 31$ scales transversely between the first dorsal spine and the anus, the 213-mm fish has $6\frac{1}{2} + 1 + 32$. The larger fish has a pectoral formula of i,14–i,14,i; the smaller has i,14,i in both pectorals. Schultz (1958:328) gives a pectoral formula of ii, 13 for Japanese *maculata*, but does not state the number of specimens examined or the range of variation in this character.

The teeth of *maculata* are needle-like and are closely set in bands on the dentary, premaxil-

lary, vomer, and palatines. They are retrorse and depressible posteriorly. The tongue bears tiny asperities which cannot be felt with the finger but which crepitate when probed with a needle. The anterior nostril lies in a simple thin-walled tube about 2.5 mm in length; the posterior nostril is kidney-shaped and has a raised rim.

Measurements (in mm) made on the 214- and 213-mm specimens, respectively, are: head length 82, 83; snout length 24.2, 23.0; eye diameter 14.4, 15.3; snout to dorsal origin (diagonal) 96, 91; length of dorsal base 85, 85; snout to anal origin (diagonal) 157, 155; length of anal base 31.4, 29.3; longest D spine (third) 24.0, 21.8; longest D ray (seventh) 43.5, 43.0; longest A spine (third) 21.3, 21.7; longest A ray (fourth) 40.7, 39.8; longest pectoral ray (fifth from top) 58.6, 54.8; longest pelvic ray (second) 37.4, 40.3; width of bony interorbital 17.1, 15.0; greatest depth of body 64, 64; and least depth of caudal peduncle 35.9, 34.7.

The 214-mm fish was frozen after capture, and thawed and photographed three days later. Its colors were as follows, based on a 35-mm transparency. Ground color pink; upper sides and back covered with numerous scattered red, dark-red, and yellow spots about size of pupil, yellow spots tending to form lengthwise stripes across snout and opercle. Lower sides, belly, and breast plain pink. Anal and spinous dorsal pink, the tips of the rays yellow; soft dorsal pink with dark-red spots and narrow yellow edge; pectorals light red, the upper rays yellow; outer caudal rays yellow, inner rays pink, spotted with dark-red. Iris red with traces of yellow.

In alcohol this fish is pale straw-colored except for what were formerly the dark-red spots on its upper sides, head, and caudal fin. These persist as brown spots. The longest dorsal, anal, pelvic, and caudal rays are narrowly tipped with black.

The two Hawaiian *maculata* fit the description and figure of the Japanese type specimen described by Steindachner and Döderlein (1883: 234), and also agree with *maculata* as set forth in the keys of Okada and Matsubara (1938:197–198) and Matsubara (1955:621). There are slight differences in proportions between Hawaiian and Japanese specimens in that the Hawaiian form tends to be slightly slimmer, its lateral line is highest beneath the fourth and fifth dorsal spines (instead of the sixth or seventh), and the last dorsal spine is only slightly less than half the length of the longest dorsal ray (rather than “much shorter” than half this ray).

P. maculata can be distinguished from *aurora*, the other Hawaiian *Pikea*, by the following characters. *P. maculata* has anal rays III, 8; 64–70 pores in the lateral line; 8 gill rakers on the first arch; and is marked anteriorly and posteriorly with spots about the size of the pupil. *P. aurora* has anal rays III, 9; 48–51 pores in the lateral line, 21 rakers on the first gill arch, and numerous tiny spots, the largest about $\frac{1}{3}$ pupil diameter in width, posteriorly on the body. Some of these data are from Schultz (1958:327) and from a specimen of *aurora* loaned by Dr. Gosline.

The 214-mm fish has been deposited in the U. S. National Museum (No. 198225).

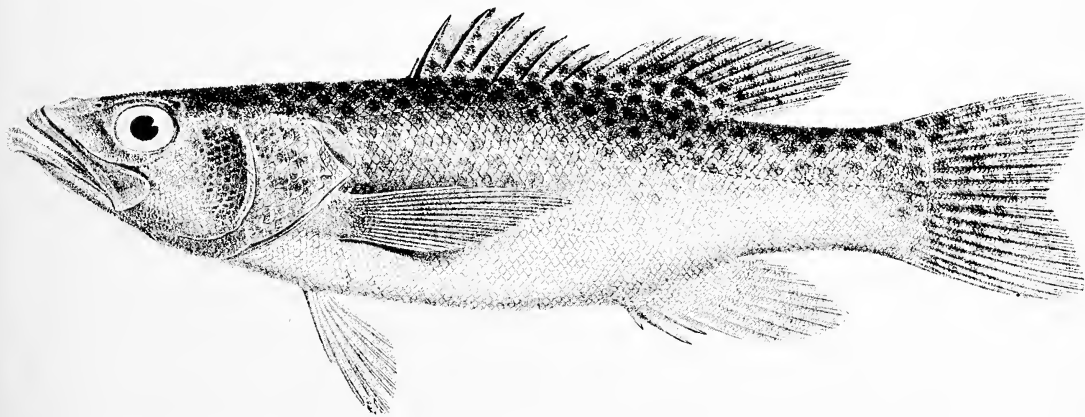


FIG. 2. Type of *Pikea maculata*, 25 cm total length. (After Steindachner and Döderlein.)

FAMILY BLENNIIDAE

Strasburg (1956:257) first recorded *Omobranchus elongatus* (Peters) from Hawaii on the basis of four specimens collected under peculiar circumstances. These fish were obtained from a concrete experimental tank located on Coconut Island, Kaneohe Bay, Oahu. The tank was supplied with running sea water, and at various times it housed experimental tunas, surgeonfish, exotic *Tridacna* clams, and other animals. The four *Omobranchus* were captured in the tank following draining; none have been taken since, in spite of years of intensive collecting in the Coconut Island area and elsewhere. It will probably never be determined how *Omobranchus* reached Hawaii, but the fact that one of the four original specimens was quite small suggested that it had been hatched in Hawaii, and that breeding populations therefore exist.

Mr. Joseph Harada, of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, obtained a fifth Hawaiian specimen of *O. elongatus* on June 16, 1963. The fish emerged from a cavity in a lump of coralline rock when the rock was immersed in fresh water to clean it. The rock had been removed from a dead reef in Pearl Harbor, Oahu, at low tide two days earlier.

This newest Hawaiian *O. elongatus* agrees with the four specimens reported earlier. It is 56.3 mm in standard length, and is a male, judging from the ocellus in its soft dorsal. No gonad could be found. Counts made on it are D XII, 19; A II, 20; P 13-13; and number of pectoral rays encompassed by gill openings 6-6. It has a relatively short digestive tract for a blenny, and this was found to be packed with filamentous red, green, and blue-green algae along with large amounts of detrital matter and diatoms. Although *Omobranchus* has a prominent fang at the corner of each jaw, apparently it is a grazing herbivore. Perhaps the fangs aid in freeing algae from their attachments.

The capture of this specimen from an open reef in Pearl Harbor, on the opposite side of Oahu and 18 miles distant from Coconut Island, confirms the presence of native *O. elongatus* in Hawaii. Obviously its habitat has not been sampled very well. The specimen has been deposited in the U. S. National Museum (No. 198223).

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Histogenesis in Roots of *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole

B. C. ARNOLD¹

AN INDIGENOUS EVERGREEN TREE, *Nothofagus solandri* var. *cliffortioides*, forms forests which dominate mountainous regions of New Zealand. The character of the root system varies according to the degree of mycorrhizal infection (Arnold, 1960). Mycorrhizal roots are much branched and stunted by comparison with uninfected roots (Fig. 1). In cross-section mycorrhizal roots are seen to be enveloped by a mantle of hyphae which penetrate in the form of a Hartig net between the radially elongated epidermal cells (Fig. 2).

Maximum development of mycorrhizas is found where leaf-mold, moss, and humus are abundant on the forest floor, and the highest incidence of fleshy non-mycorrhizal roots is found in boggy soil, or when the tree is grown in cultivation in heavy garden loams.

The present investigation was undertaken to determine whether or not the apical organization of *Nothofagus* mycorrhizas differed from that of uninfected roots, and to compare the histogenetic pattern of *Nothofagus* roots with that of the European beech *Fagus sylvatica*.

I am indebted to the University Grants Committee for a research grant in aid of this work.

METHODS AND MATERIALS

Uninfected roots and mycorrhizas were fixed at fortnightly intervals throughout the year in the following solutions: tannin fixative (Johansen, 1940); chromium sulphate fixative (Johansen, 1940); cytoplasmic fixative (Marengo, 1952); formo-acetic alcohol (Johansen, 1940); Bouin's fixative (Baker, 1950); acetic alcohol (Darlington and La Cour, 1947).

Dehydration was carried out in a closely graded series of ethyl alcohol; clearing was done

in alcohol-benzene mixtures; the specimens were embedded in paraffin; and serial sections were cut at 10 μ .

The following stains were employed: anilin blue + safranin (Johansen, 1940); methyl violet + erythrosin (Johansen, 1940); methyl violet + eosin (Johansen, 1940); Crystal violet, chromic method (Darlington and La Cour, 1947); Feulgen technique for slides (Darlington and La Cour, 1947); Chlorazol black E + Aceto carmine (Nebel, 1940); Chlorazol black E (Cannon, 1941); Iron-alum ammonium sulphide (Wigglesworth, 1952).

This wide range of fixatives and stains was employed in an attempt to determine whether the hypodermis of mycorrhizas contains living substance or whether it is in fact relatively empty of protoplasmic content.

OBSERVATIONS

In uninfected roots of *Nothofagus solandri* var. *cliffortioides* the meristematic regions which give rise to epidermis, cortex, stele, and rootcap are readily distinguishable (Fig. 3) and their arrangement is similar to that reported for *Fagus sylvatica* (Clowes, 1961). While it is convenient to refer to these tracts of meristematic cells as dermatogen, periblem, plerome, and calyptragen, respectively, I have been unable to conclude whether or not they represent entirely discrete histogens in the original sense of the word.

Despite the very considerable histological modification of root structures in mycorrhizas, including a reduction in the size of the promeristem, it is possible to identify in them a dermatogen, periblem, plerome, and vestigial calyptragen in much the same relationship as in uninfected roots. The maturation of derivatives of the promeristem of mycorrhizas is greatly accelerated, and the derived cells are often reduced in number.

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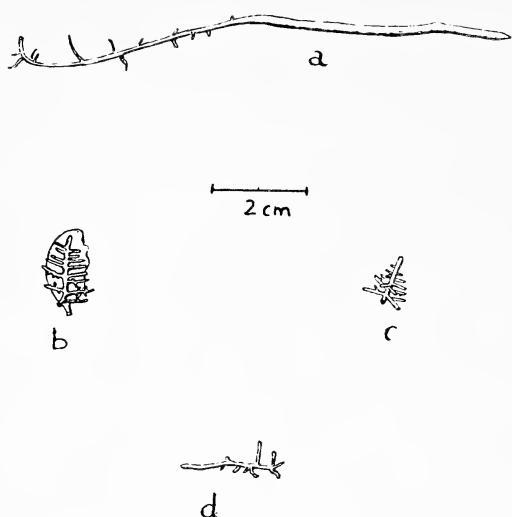


FIG. 1. *a*, An uninfected root, *b*, *c*, and *d*, mycorrhizas. All life size.

The rootcap of mycorrhizas is usually reduced to a single layer of cells confined on the outside by the fungal mantle which sheathes the whole apex and penetrates the later-formed epidermal cells.

Differentiation of the epidermis of mycorrhizas is initiated very much closer to the promeristem than is the case in uninfected roots, and is characterized by crowded divisions in the radial plane, the walls being as close together as $2.5\ \mu$ in fine mycorrhizas, and slanting in a forward direction (Fig. 4). Clear vacuoles appear in the developing epidermal cells but are later replaced by an opaque mass which fills the cells completely. This opaque mass absorbed all of the stains to which the sections were subjected.

In large mycorrhizas the cortex may contain two or three layers of cells, but in finer mycorrhizas it may be reduced to a single layer or even replaced by the hypodermis (Fig. 5). Vacuolation of precursor cells of the cortex takes place earlier in mycorrhizas than in non-mycorrhizal roots. The vacuoles are at first clear, as is best shown by fixation in Marengo's cytoplasmic fixative (Marengo, 1952). Later the cortical cells of mycorrhizas become filled with an opaque homogeneous material which absorbs stains avidly. Millon's test for protein in mature cortical cells was positive and strong.

The staining reactions of the endodermis are similar to those of the cortex and epidermis but more intense. Vacuolation in the endodermis of mycorrhizas is precocious, as it is in the other tissues, and there is an early deposition of tannin in the endodermis.

Maturation of stelar tissues occurs much closer to the promeristem in mycorrhizas than in mycorrhiza-free roots.

All the foregoing histological characteristics of mycorrhizas of *N. solandri* var. *cliffortioides* are closely similar to those of mycorrhizas of *F. sylvatica* as reported by Clowes (1951), but one outstanding feature of *Nothofagus* mycorrhizas which has not been reported for *Fagus* is the peculiar histogenetic pattern of the hypodermis.

Vacuolation of the precursor cells of the hypodermis in mycorrhizas of *Nothofagus* takes place well in advance of vacuolation of the stelar cells.

The first formed cells of the hypodermis are conspicuous extremely close to the promeristem. The cytoplasm shrinks against the walls to a lens-shaped blob in which the nucleus is embedded, and finally the entire protoplasmic content disappears. In longitudinal section an irregular line of clear cells can be seen leading back to a definite file of cells with thin buckled walls (Fig. 4).

Despite the use of a wide range of fixatives and stains, the mature hypodermis appeared quite devoid of protoplasmic content.

Hyphae were not found at any stage to enter this clear-layered hypodermis, which appears to be a barrier to further fungal invasion of the root.

DISCUSSION

Notwithstanding the undecided question of whether the meristematic layers which give rise to epidermis, cortex, stele, and rootcap in *N. solandri* var. *cliffortioides* are discrete histogens in the original sense of the term (Clowes, 1961), it is clear enough that in roots of *Fagus* and *Nothofagus* there exists the same fundamental type of organization of the apical meristem, which is consonant with the phylogenetic relationship of the two genera.

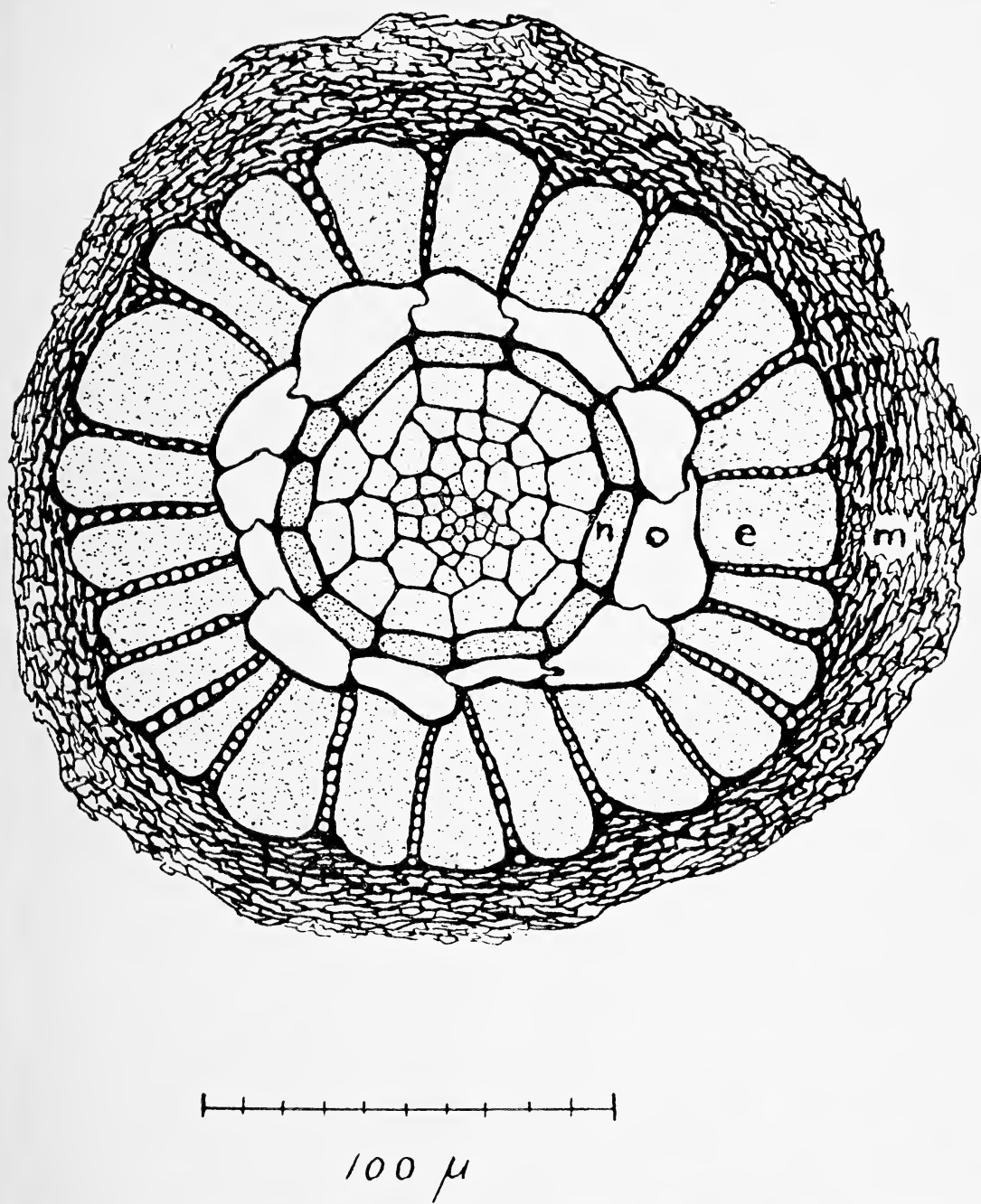


FIG. 2. Cross section of a mycorrhiza. *n*, Endodermis; *o*, clear hypodermal cells; *e*, epidermis; *m*, mantle.

Furthermore, it is evident that mycorrhizal infection does not alter the basic disposition of dermatogen, periblem, plerome, and calyptragen in *Nothofagus* roots. The promeristem of mycorrhizas is reduced but not damaged or incapacitated. Not infrequently the apical meristem regains sufficient vigor to break through the fungal mantle and give rise to non-mycorrhizal roots, indicating a dynamic balance of growth of root and fungus.

It has been suggested earlier (Arnold, 1959, 1960) that the histological modifications found in *Nothofagus* mycorrhizas are consistent with the hypothesis that the mycorrhizal fungus exudes auxins or auxin-like substances which are a dominant factor in the morphogenesis and growth of *Nothofagus* roots. No doubt there are other accompanying effects of the presence of the fungal mantle over the tissues of the infected roots.

In the very thorough study of mycorrhizas of *Fagus sylvatica* made by Clowes (1951), no mention is made of the structure and differentiation of the hypodermis. Morrison (1956), who

studied the mycorrhizal condition in *Nothofagus menziesii* (Hook. f.) Oerst., noted without further comment that in uninfected roots "the hypodermal layer consists of thin walled clear cells while the inner layer of the cortex consists of thick walled cells." No mention was made of the presence or otherwise of a hypodermis in mycorrhizas.

In uninfected roots of *Nothofagus solandri* var. *cliffortioides* a hypodermis of clear cells has been seen in transverse sections of some specimens but not in others, and it is presumed that Morrison's observations were based on transverse sections probably somewhat remote from the apex. This presumption is made from observations on longitudinal sections of uninfected roots of *N. solandri* var. *cliffortioides* in which no instances of a clear hypodermis were found even as far back as 1.5 cm from the promeristem. Vacuolation in the hypodermis of non-mycorrhizal roots of *N. solandri* var. *cliffortioides* is very much more gradual than in mycorrhizas.

On the basis of the present observations on the histology and developmental pattern of the

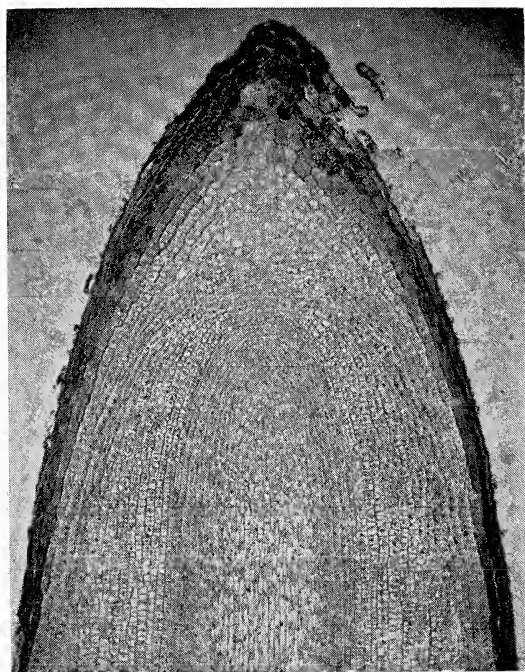


FIG. 3. Longitudinal section of uninfected root, $\times 80$. There is no premature differentiation of tissues as shown in Figure 4.

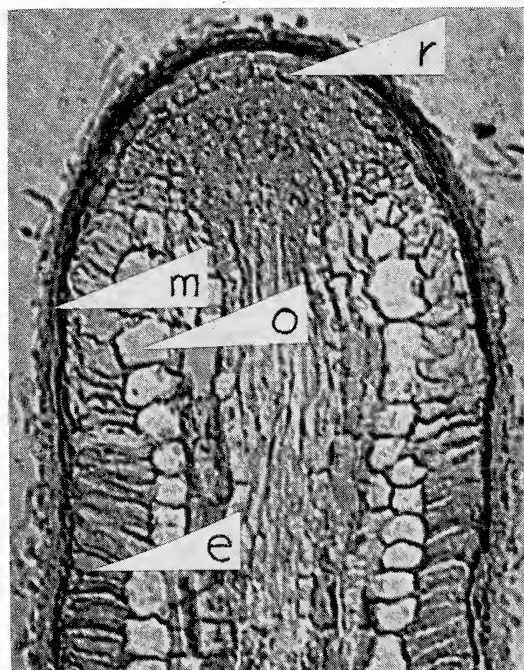


FIG. 4. Longitudinal section of a fine mycorrhiza, $\times 120$. *m*, Mantle; *e*, epidermis; *o*, hypodermis; *r*, rootcap.

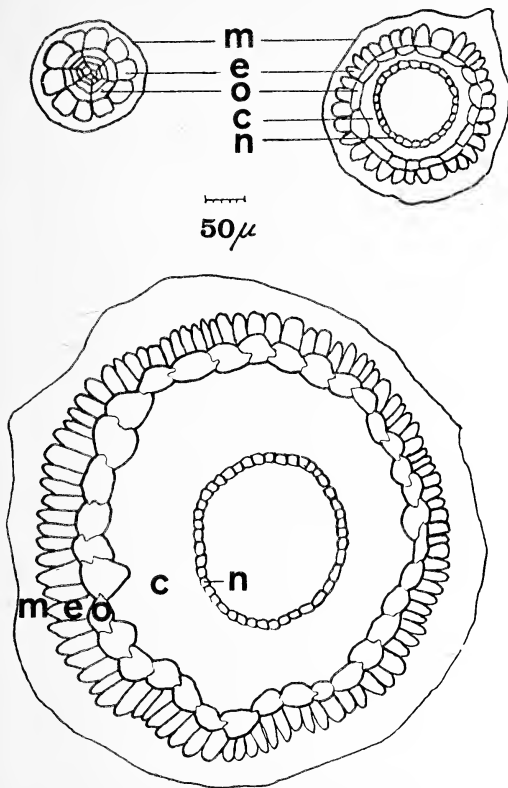


FIG. 5. Outline sketches of transverse sections of three mycorrhizas showing range in reduction of diameter and cell number. *m*, Mantle; *e*, epidermis; *o*, hypodermis; *c*, cortex; *n*, endodermis.

hypodermis of mycorrhizas of *N. solandri* var. *cliffortioides* it is suggested that the hypodermis plays an important role in preventing the further penetration of the fungus into the inner tissues of the root.

SUMMARY

The root apical meristem of *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole is similar to that of *Fagus sylvatica*.

In both genera the organization of meristematic cells which give rise to epidermis, cortex, stele, and rootcap is basically unaltered by mycorrhizal infection.

However, the subsequent maturation of tissues in mycorrhizas and non-mycorrhizal roots differs considerably.

A noteworthy feature of mycorrhizas of *N. solandri* var. *cliffortioides* is the lack of protoplasmic content of the hypodermis, and its striking mode of differentiation from the promeristem.

It is suggested that the hypodermis plays an important role in excluding mycorrhizal fungi from further penetration of *Nothofagus* roots.

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Two New Mites (Acarina: Laelapinae) from Oriental Insectivores (Mammalia: Insectivora)

E. W. JAMESON, JR.¹

ABSTRACT: The two species described are closely allied parasites of shrews (*Anourosorex squamipes* and *Soriculus fumidus*) from Taiwan, and of a mole (*Urotrichus talpoides*) from Japan (Honshu, Shikoku, and Kyushu). The similarity of these two species indicates a common geographic origin of the hosts, and suggests that there are probably allied species of these mites on the Chinese mainland. These two species of *Haemolaelaps* appear most closely related to the *ulysses* group, three species from Australian marsupials.

A DISTINCTIVE MESOSTIGMATIC MITE is a characteristic parasite of shrews of Taiwan, and another closely related species parasitizes shrew-moles of Japan. These two species, which are described below, seem to be rather close to the *ulysses* group recently described and defined by Domrow (1964), but they differ in some features. Both have the following characters which, collectively, separate these mites from other species of *Haemolaelaps*, including those of the *ulysses* group:

Small, delicate laelapine mites, with legs rather short and body subovoid. Epigynial plate slightly expanded posteriorly, bearing only the anteriormost pair of setae. Anal plate broader than epigynial plate, at least as broad as long and concave anteriorly. Gnathosoma and chela typical for laelapine mites; pilus dentilis broadened, and as long as fixed digit. Palpal trochanteral seta not inflated. Dorsal plate covering most of dorsal body surface; with 35 or more pairs of minute setae. Setae on coxae II and III not expanded and hyaline. Femora and trochanters without apically notched setae.

Haemolaelaps soricinus, n. sp.

DORSUM (Fig. 1 A): Dorsal plate ovoid (wider posteriorly), with 35 pairs of minute setae, only the caudalmost being distinctly longer than the others. Shoulders reduced. With several small pores as illustrated. Soft parts with about 10 pairs of setae.

VENTER (Fig. 1 E): Sternal plate (Fig. 1 B) with the anteriormost pair of setae distinctly in front of the anterior margin; anterior margin rounded and convex. Sternal setae rather short and delicate, not extending beyond base of posteriorly adjacent setae. Epigynial plate expanded posteriorly to about the distance between coxae IV. Anal plate (Fig. 1 D) wider than epigynial plate, wider than long, and anterior margin concave and rounded; anus, anal and adanal setae on caudal half of anal plate. Coxae and legs rather stout; setae not heavy. Coxae without spurs; coxa II without anterior marginal spur. Peritremal plate not with a detached sclerite extended around coxa IV.

GNATHOSOMA (Fig. 1 C): Deutosternum with six or seven rows of teeth of one or two teeth each. Chela (Fig. 1 F) with a circlet of five or six hyaline hairs subtending the movable digit; a single curved hair at the base of the fixed digit. Fixed digit with a broad curved pilus dentilis. Tectum apparently bilobed, with a longitudinal groove or grooves.

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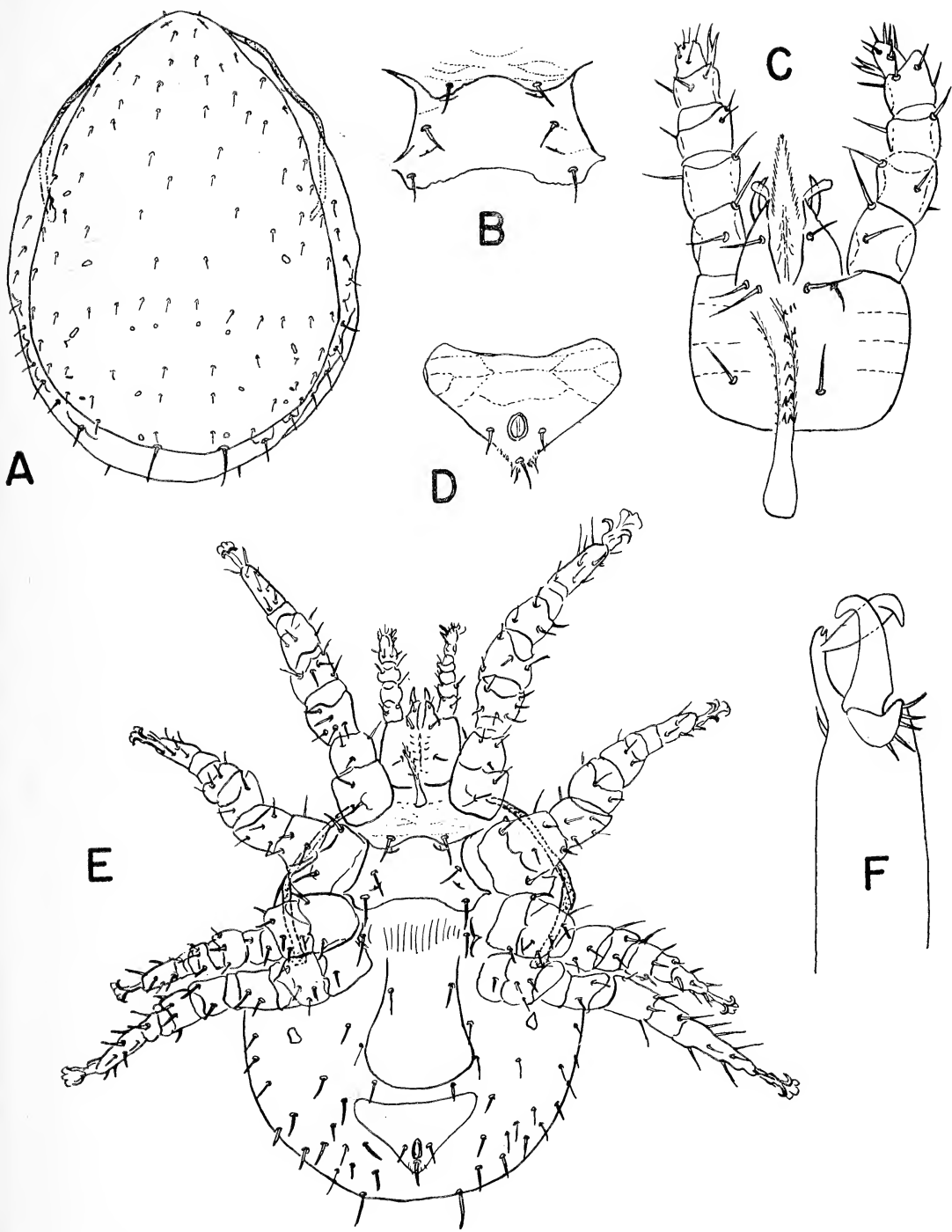


FIG. 1. *Haemolaelaps soricinus*. A, Dorsum; B, sternal plate; C, gnathosoma; D, anal plate; E, venter; F, chela.

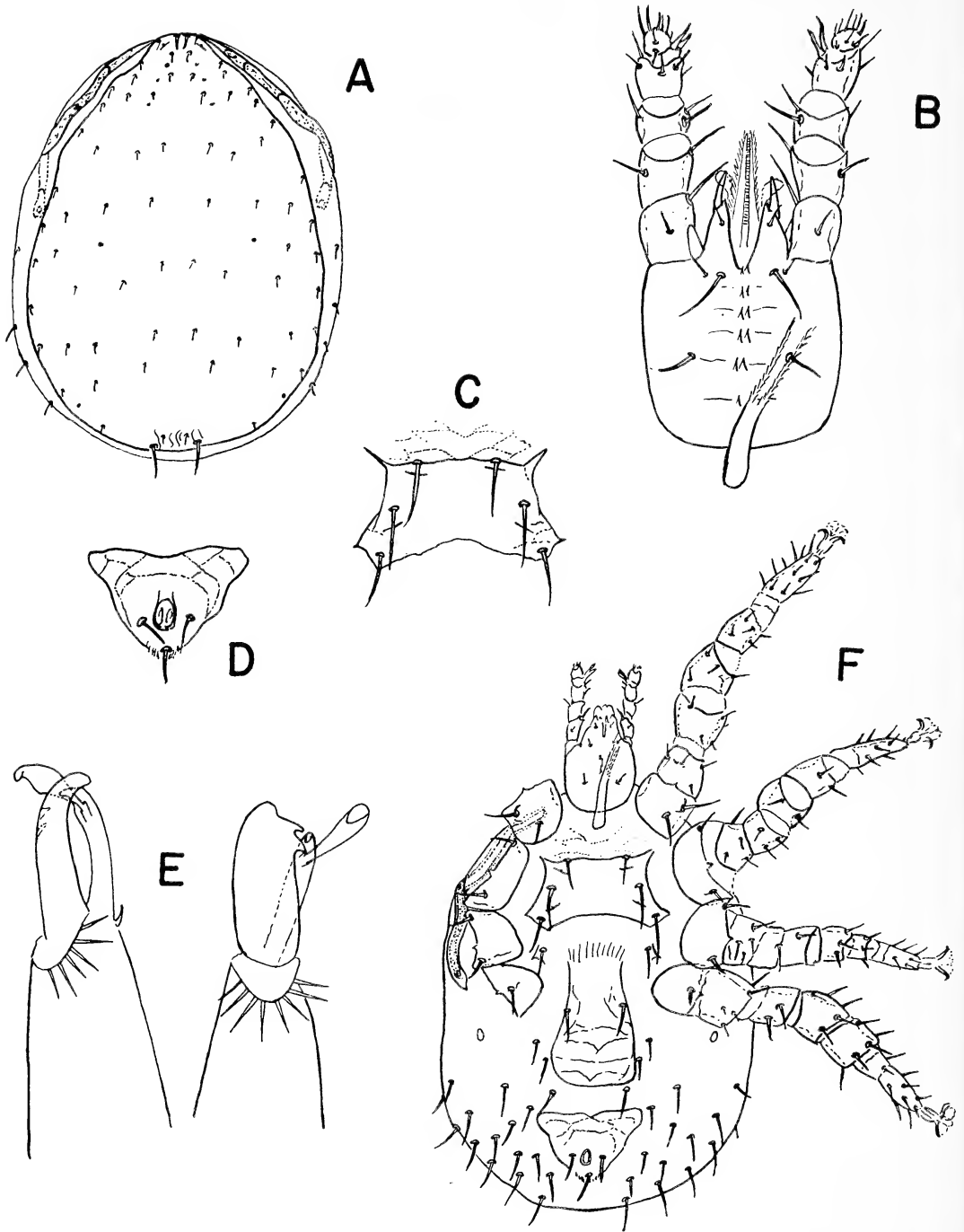


FIG. 2. *Haemolaelaps himizu*. A, Dorsum; B, gnathosoma; C, sternal plate; D, anal plate; E, chela; F, venter.

TYPE: Holotype female ex *Anourosorex squamipes*, 10 miles east of Wu-She (6,400 ft elevation), Nan-T'ou Prefecture, Taiwan, 19 October 1963. Paratype females: one with same data as type; one from type host and type locality, 25 July 1963; one from type host, Ali Shan, Chia I Prefecture, 19 February 1965; three females ex *Soriculus fumidus*, Ali Shan, Chia I Prefecture, 19 February 1965. All collected by the author. Holotype deposited in the U. S. National Museum. Paratypes deposited in the Bernice P. Bishop Museum, the Queensland Institute for Medical Research, and the Rocky Mountain Laboratory.

Haemolaelaps himizu, n. sp.

DORSUM (Fig. 2 A): Dorsal plate ovoid (wider posteriorly), with 41 pairs of minute setae (caudalmost dorsal setae are somewhat longer). Dorsal plate with several short grooves or fissures between caudalmost dorsal setae. Soft parts with 4 pairs of setae.

VENTER (Fig. 2 F): Sternal plate (Fig. 2 C) with anteriormost setae barely on plate; anterior margin slightly and irregularly convex. Sternal setae long, projecting beyond base of posteriorly adjacent setae. Epigynial plate expanded posteriorly almost to distance between coxae IV. Anal plate (Fig. 2 D) wider than epigynial plate, wider than long; and with anus, anal and adanal setae on caudal half of anal plate. Anal plate distinctly concave on anterior margin. Coxae and legs rather stout. Peritremal plate not with a detached sclerite extending around coxa IV.

GNATHOSOMA (Fig. 2 B): Deutosternum with six rows of teeth, each row of two (sometimes one) teeth. Chela (Fig. 2 E) with a circlet of six to eight hyaline hairs subtending the movable digit; a single hair at the base of the fixed digit. Tectum folded at anterior margin so that it is three-lobed (or apparently so).

TYPE: Holotype female ex *Urotrichus talpoides* Temminck, from Ohara, Kyoto-Fu, Honshu, Japan; 6 March 1952. Paratypes, from type host: one female, Hanase, Kyoto-Fu, 10 June 1952; one female, Hanase, Kyoto-Fu, 1 August 1952. All collected by the author. Two additional females, not designated as paratypes, from "Camp Fuji" (lower slopes of Mt. Fuji). Holotype deposited in the U. S. National Museum. One paratype in Bernice P. Bishop Museum; one paratype in collection of the author. The two additional specimens are in the collection of the Department of Entomology, Walter Reed Army Medical Hospital.

The name *himizu* is the Japanese name for the host.

COMMENT: The occurrence of these two related parasites on Taiwan shrews and a Japanese shrew-mole suggests that additional allied species of *Haemolaelaps* may occur on the Chinese mainland on the complex of soricoid insectivores.

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Studies of Food Preference in Algivorous Invertebrates of Southern California Kelp Beds¹

DAVID L. LEIGHTON

ABSTRACT: Stands of the giant kelp, *Macrocystis pyrifera*, frequently suffer attack by grazing organisms and in some cases complete destruction has been observed. The present investigation of the feeding habits of grazing organisms is primarily concerned with food preferences. Discrimination in choice of plant foods was examined in 11 common invertebrate species of the sublittoral rock bottom fauna of southern California by measuring the differential consumption of seven common algal species in the laboratory. The algae were selected as representing the major floral elements of the kelp bed (*Macrocystis pyrifera*) community. All of the grazers exhibited high degrees of preference for *Macrocystis*. Shallow water grazers revealed stronger preferences for *Egrecia* than for *Macrocystis*. Herbivores found at greater depths indicated strongest preferences for *Macrocystis*, *Laminaria*, and *Pterygophora*, plants that are generally common at these depths. The deepest-living herbivore, *Lytechinus*, showed greatest preference for a red alga, *Gigartina*; red algae generally supplant brown algae in dominance at greater depths. Some of the invertebrates refused certain of the marine plants. A specific distaste factor may exist in these cases.

THE LARGE LAMINARIAN BROWN ALGA, *Macrocystis pyrifera*, has attracted interest during the past decade since it became apparent that the once extensive beds of this plant were on the decline in southern California and northern Baja California (North, 1962, 1963:7). A five-year study of the kelp beds was undertaken at the Scripps Institution of Oceanography (Institute of Marine Resources) to seek causes of the kelp regression. (The final report is in preparation.) Physical and chemical factors possibly detrimental to kelp, e.g., elevated temperature and high turbidity of nearshore water and toxicity associated with industrial wastes discharged into the sea, are discussed elsewhere (North, 1963). Studies of food habits and behavior of kelp-associated fauna were prompted when it was found that grazing by organisms normally a part of the kelp community was frequently a cause of kelp destruction (Leighton, 1960; North, 1963). Because gut contents provide unreliable clues to food habits in algivorous animals,

studies were carried out in marine laboratory aquaria where food selection could be observed.

Studies of algal preferences in the marine snail, *Littorina obtusata*, considered chiefly scent perception and orientation to algae which were variously distributed within large tanks in which slow unidirectional water flow was usually maintained (Barkman, 1955; Van Dongen, 1956; Bakker, 1959). The present study and an earlier one (Leighton and Boolootian, 1963) report gustatory preference and quantitative measurement of the amounts of algal foods ingested. The method reflects more certainly the animals' genuine food preference in contrast to selection of algae through other motivation (e.g., for spawning substrate, specific plant shelter, etc.). Barkman (1955:50) states that *L. obtusata* deposits its eggs on fronds of Fucaceae, particularly on *Fucus serratus*.

MATERIALS AND METHODS

The procedure employed was simple. Groups of a grazing species, held either in large concrete tanks or in glass aquaria, were provided equal weights of each of several common algae occurring in or near kelp beds. Amounts ingested

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were determined by measuring loss in weight of algae after a feeding period. Data were tested statistically for consistency of ranks and for significant differences in means of consumption values. The method and its analysis are considered to be an improvement over that reported earlier (Leighton and Boolootian, 1963).

The following 11 common benthic invertebrates, known to be exclusively or predominantly macro-herbivores, were studied:

Echinoids

Lytechinus anamesus Agassiz and Clark
Strongylocentrotus franciscanus Agassiz
Strongylocentrotus purpuratus (Stimpson)

Gastropods

Aplysia californica Cooper
Astraea undosa (Wood)
Haliotis corrugata Gray
Haliotis fulgens Philippi
Haliotis rufescens Swainson
Norrisia norrisii (Sowerby)

Crustacea

Pugettia producta (Randall)
Taliepus nuttallii (Randall)

The animals were collected from a variety of habitats and depths to insure that the results obtained would not reflect conditions imposed by the environment in any single habitat. Individuals employed varied about an average adult size found in the field. During the years 1960 and 1961 at least 10 experiments were run with each grazing species. Numbers of animals in experiments ranged from 2 to 10 depending on the size of the particular species.

The following seven species of algae were employed, representing the major noncalcareous plants available to grazers in southern California kelp beds in terms of biomass (Dawson et al., 1960):

Phaeophyta

*Cystoseira osmundacea*² (Turner) Agardh

² *Halidrys dioica* Gardner is indistinguishable from *Cystoseira osmundacea* when fruiting organs are not present (Dawson et al., 1960) and both forms have undoubtedly entered the experiments. The low preference values observed for *Cystoseira-Halidrys*, in most cases, suggests there is no serious objection to the chance mixing of the two forms as one. Most experiments were performed in late winter, spring, and summer when fruiting organs permitted distinction of these two species.

Egregia laevigata Setchell
Eisenia arborea Areschoug
Laminaria farlowii Setchell
Macrocystis pyrifera (L.) Agardh
Pterygophora californica Ruprecht
Rhodophyta
Gigartina armata Agardh

Blotted fresh blades or fleshy thalli were cut either into pieces about 4 cm square or into 2.5 cm discs. Equal weights of the seven algae were then thoroughly mixed and placed in experimental and control containers alike. In most cases the quantity of food provided aggregated 70 g, comprising 10 g of each species. Larger grazers were offered twice this amount. The controls, containing algal pieces prepared in the same manner, but no grazers, provided a measure of any weight changes due to decomposition and/or imbibition. Experiments were of 24 hr duration. All algal pieces sank and remained on the bottom within easy reach of all the animals; pneumatocysts were excluded.

A number of precautions were taken to assure uniformity in responses and to maximize random contacts between animals and seaweed fragments:

1. Freshly collected algae were always used.
2. A free flow of water was maintained continuously in the containers.
3. The algal pieces were thoroughly mixed several times during each experiment.
4. Numbers of grazers and sizes of containers were selected so that each food species should be equally within reach of each individual.
5. After one to three experiments, grazers were replaced by newly collected individuals.
6. Between experiments animals were allowed to feed on a variety of algae but were subjected to approximately two days' starvation immediately prior to each experiment.
7. Feeding experiments were suspended during times of unusually high ambient water temperatures. (Algal deterioration was most evident at temperatures above 20 C.)

At the end of a feeding period all remaining algal fragments were removed from each tank, segregated as to species, blotted free of adhering water, and weighed to the closest decigram. Weight losses, corrected for changes in the con-

trols, were taken as the seaweed consumed by grazers. Weight changes in the controls were usually very small.

RESULTS

The allowance method of Tukey (1953:90) was used to test for differences in consumption. Differences between the means of algal consumption values, significant at a 5% error rate, are indicated by separate boxes in Figure 1. Plant species falling in intermediate positions and not significantly different from adjacent groups are not enclosed. In most cases three distinct levels of consumption are evident. The results show that in many cases *Macrocystis* was consumed in relatively large amounts, appearing at or near the highest level; *Cystoseira*, *Gigartina*, or *Pterygophora* were frequently, but not always, at the lowest level; and the other algal species were at intermediate levels.

Means and ranges of quantitative data for all grazers are provided in Figure 2. The ranges are, in some instances, rather great. Variations in ambient temperature between 13 and 19 C caused fluctuation in feeding rate. Sizes of animals, while similar, did vary. Other factors doubtless affected feeding rate and selection. Despite the variability, a considerable degree of correspondence was found between experiments. To test the agreement of results, a ranking method described by Kendall (1955:95) was employed. In each trial, the algae were assigned ranks from 1 to 7 in order of decreasing quantities consumed. Values of W , the coefficient of concordance, ranged from 0.41 to 0.79 (Table 1); all were significant beyond the .001 level. The order of preference of each grazing species, therefore, may be regarded as consistent and the mean values for consumption (Fig. 2) afford the best estimate of the relative degree of attractiveness of the algae to the grazing animals.

The data for the entire experimental series are included for two species, *Strongylocentrotus purpuratus* (Table 2) and *Lytechinus anamesus* (Table 3), in order to provide an indication of the intraspecific variability of results. *S. purpuratus*, collected from a variety of habitats, showed limited variation in preference behavior. Mean values for *L. anamesus* from the La Jolla

Canyon and from the Mission Bay entrance show general agreement. The same tendency toward a specific pattern of preferential response to the algae tested here was found in other grazing organisms collected from a variety of plant environments. (A recent extension of these studies has shown similarities in response by *Haliotis* and *Strongylocentrotus* collected at latitudes well beyond the range of certain of the algae used here. Hence a species-specific pattern of selection appears to exist, some species being characteristically attractive while others are not.)

Macrocystis was most highly preferred in 7 of 11 cases; typical kelp bed inhabitants fall within this group. *Egregia*, a shallow water kelp (0-8 m) was most preferred by *Norrisia*, *H. fulgens*, and *Aplysia*, all most common at lesser depths. *Lytechinus*, normally a relatively deep water dweller, preferred red algae (represented in these experiments by *Gigartina armata*). Red algae generally supplant brown algae in dominance at depths exceeding 35 m.

Several species of brown algae were consistently consumed in greatest relative quantities by all grazers. *Egregia* and *Laminaria*, in addition to *Macrocystis*, were generally favored. *Cystoseira*, on the other hand, was seldom ingested by grazers other than *Pugettia*, *Taliepus*, and *H. corrugata*. *Gigartina* was readily eaten by *Lytechinus*, *Aplysia*, *Astraea*, and *Strongylocentrotus*, but was hardly touched by *Pugettia*, *Taliepus*, *Norrisia*, and *H. corrugata*.

The coefficient of concordance (W_c) was determined for a summation of the rankings of preference for all 11 grazing species (Table 4) and is significant at better than the 0.1% level. The order of preference is, therefore, generally consistent throughout the group of species, with *Macrocystis* as the most commonly preferred item and *Cystoseira* as the least acceptable.

Since some closely allied species equipped with similar chewing, biting, or rasping organs exhibited divergent preference behavior, the results are not considered to be a consequence of relative mechanical ability to cope with a particular food. Toughness of foods might be suggested as influencing choice when measured by the techniques employed; the resilient, denser algae being consumed at a slower rate than the tenderer tissues. If this were true, one would ex-

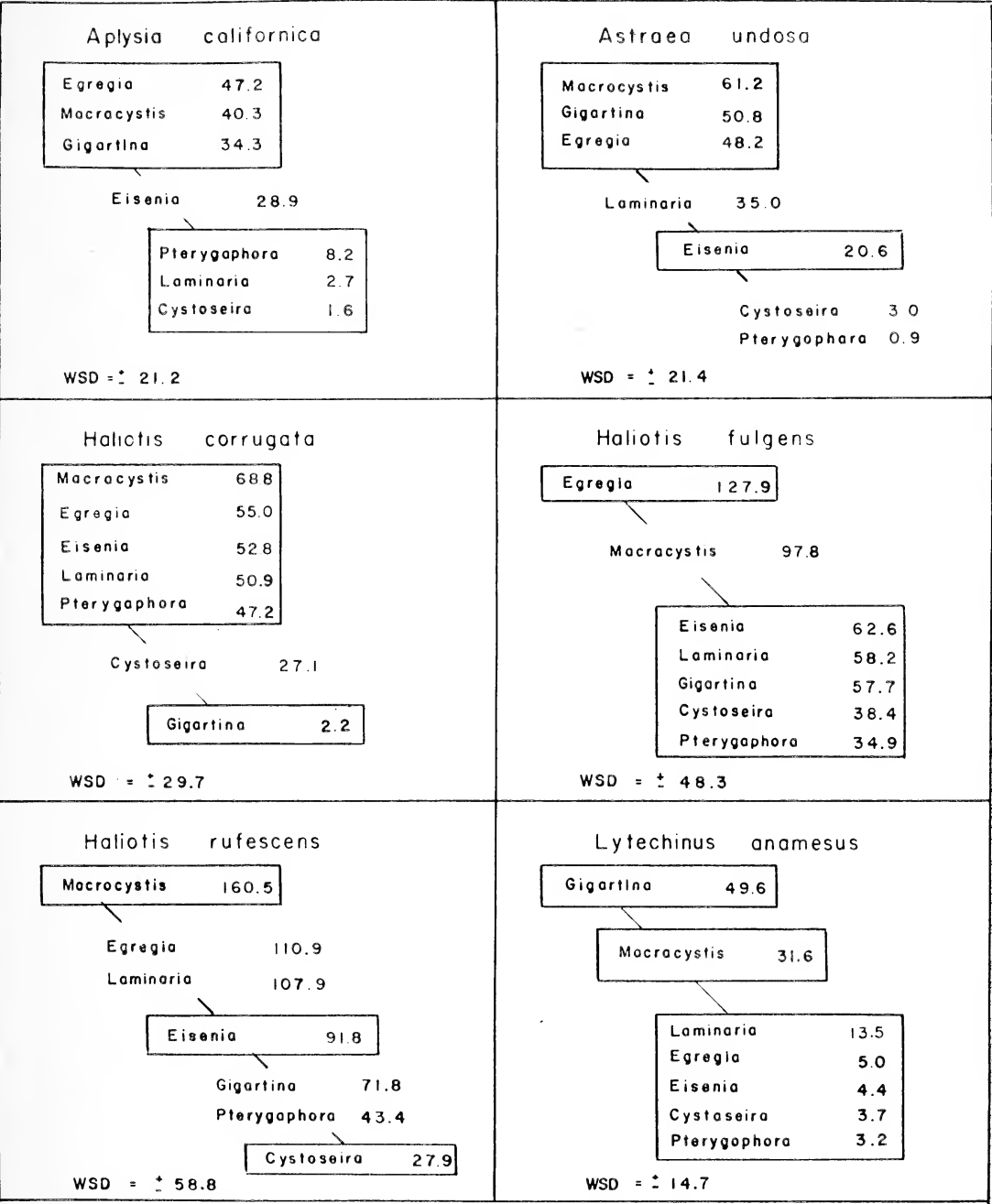


FIG. 1. Differences in amounts of various algae consumed by invertebrate grazers. Species in boxes are not significantly different (.05 level) from each other, but do differ from those in preceding or following boxes. Intermediates are not boxed. Algae are arranged from top to bottom in order of decreasing preference. WSD, the wholly significant difference, is the minimum difference between species which would be significant at the 5% level (see Tukey, 1953).

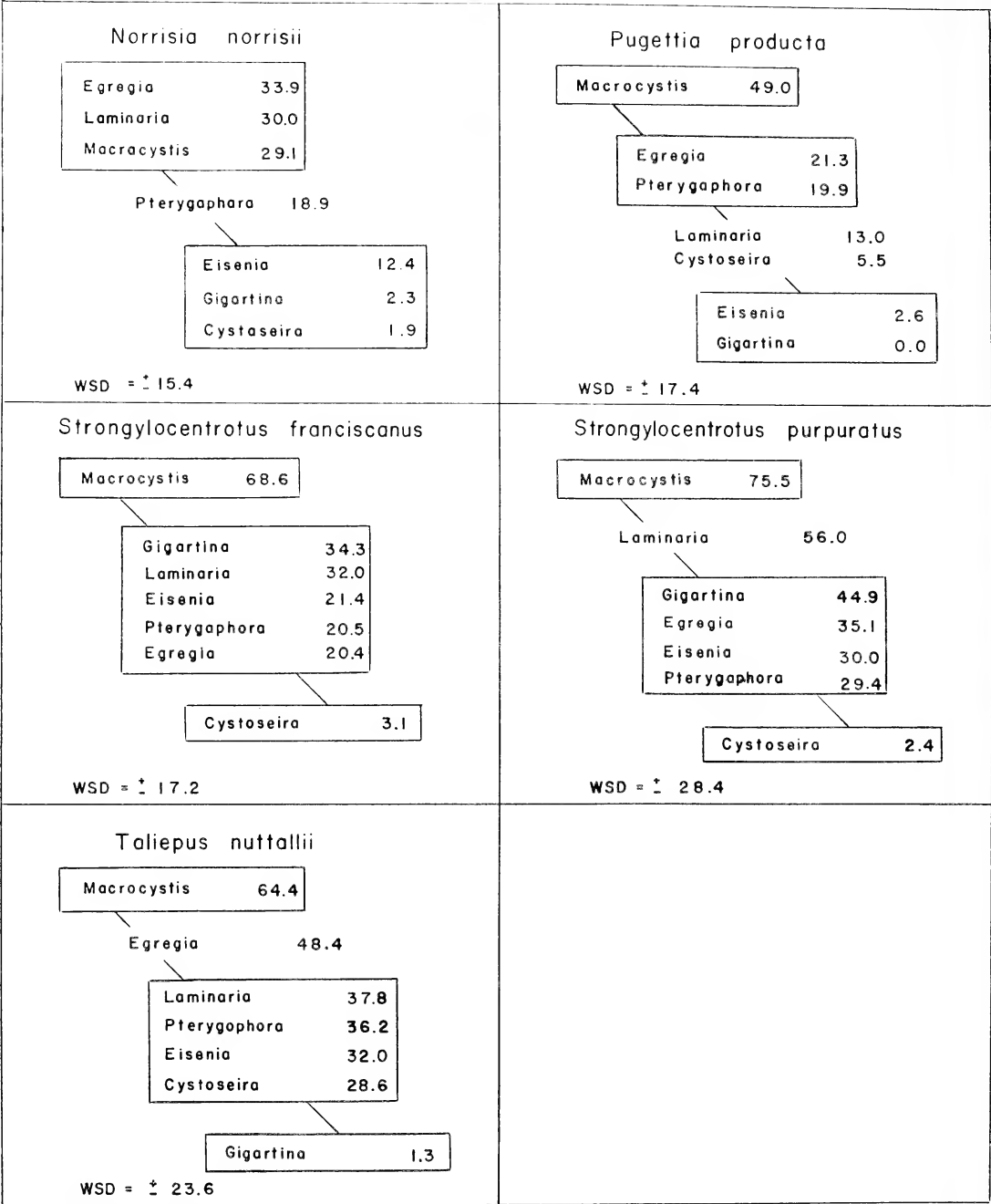


FIG. 1 (cont.). Differences in amounts of various algae consumed by invertebrate grazers.

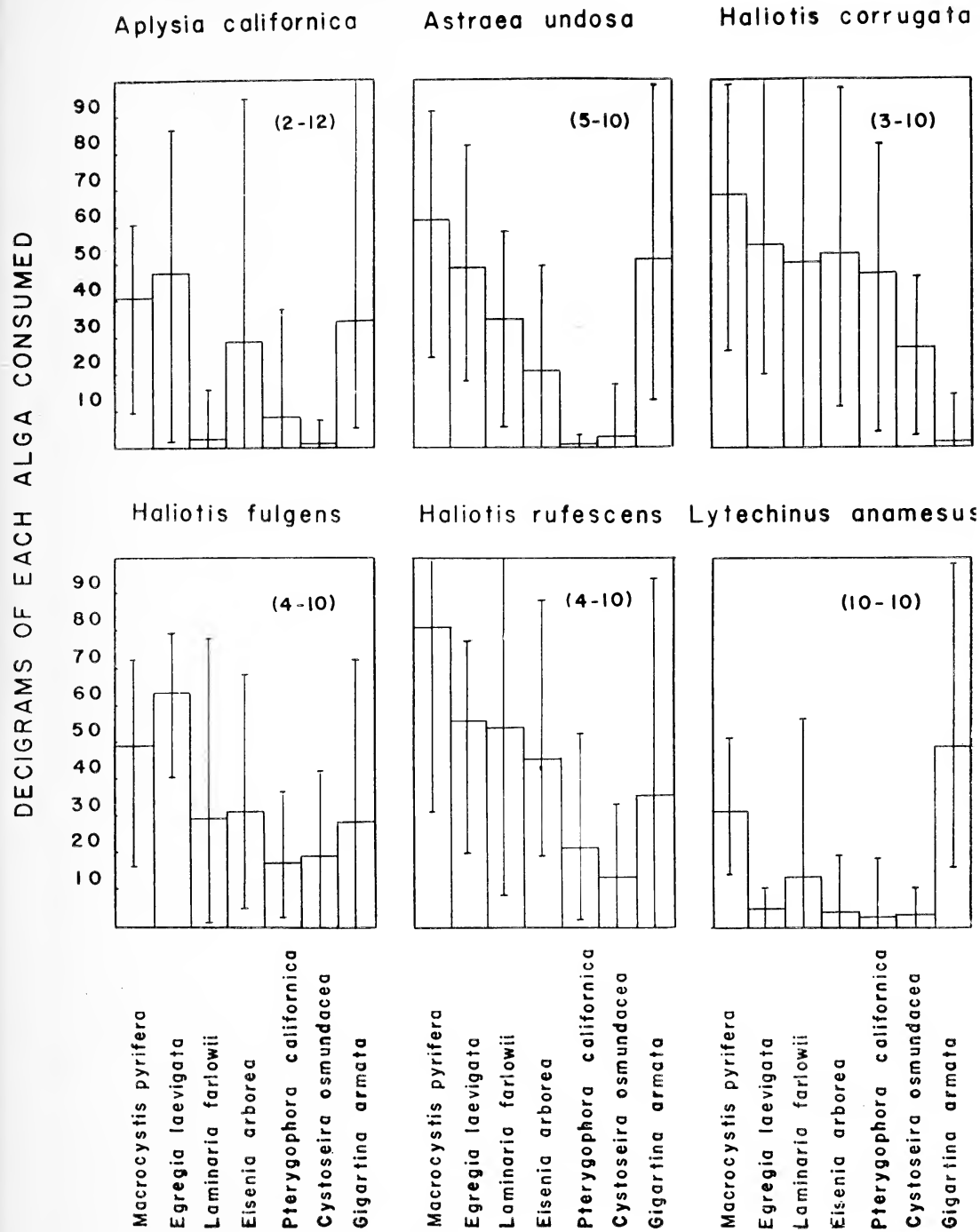


FIG. 2. Means of plant consumption values shown by histogram. Ranges are indicated by vertical lines. Consumption data for *Haliotis fulgens* and *H. rufescens* are reduced by one-half. Numbers of individuals employed and numbers of experiments are given in that order hyphenated in parentheses.

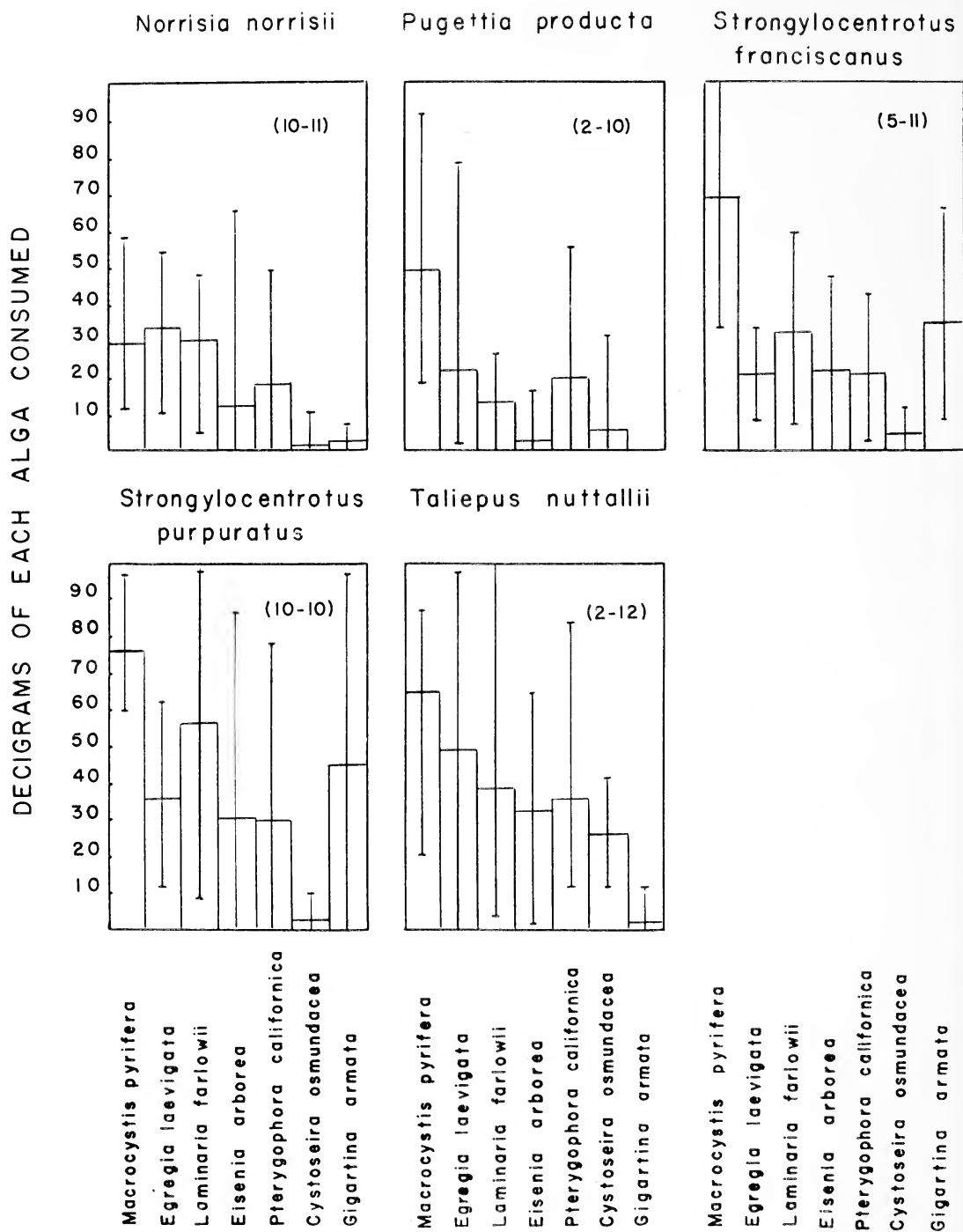


FIG. 2 (cont.). Means of plant consumption values. Ranges are indicated by vertical lines.

TABLE 1

CONSISTENCY IN RESULTS OF EXPERIMENTAL FEEDINGS OF SEVEN ALGAL FOODS TO INVERTEBRATES

INVERTEBRATE SPECIES	NUMBER OF EXPERIMENTS	NUMBER OF INDIVIDUALS EMPLOYED IN EACH EXPT.	TOTAL NUMBER OF DIFFERENT GROUPS EMPLOYED	COEFFICIENT OF CONCORDANCE* W =
<i>Aplysia californica</i>	12	2	6	0.59
<i>Astraea undosa</i>	10	5	5	0.79
<i>Haliotis corrugata</i>	10	3	3	0.51
<i>Haliotis fulgens</i>	10	4	6	0.47
<i>Haliotis rufescens</i>	10	4	5	0.58
<i>Lytechinus anamesus</i>	10	10	8	0.60
<i>Norrisia norrisii</i>	11	10	5	0.41
<i>Pugettia producta</i>	10	2	9	0.77
<i>Strongylocentrotus franciscanus</i>	11	5	8	0.58
<i>Strongylocentrotus purpuratus</i>	10	10	7	0.58
<i>Taliepus nuttallii</i>	12	2	5	0.51

* This coefficient is a measure of the degree of agreement between sets of repetitive experimental results (see text). Values may range from 0.0 to 1.0, the higher figures indicating a higher degree of agreement. All values in this table are significant at better than the 0.1% level.

TABLE 2

DECIGRAMS OF DIFFERENT ALGAE CONSUMED BY 10 ADULT *Strongylocentrotus purpuratus* IN 24-HOUR EXPERIMENTAL FEEDING PERIODS

EXPERIMENT	<i>Macrocystis</i>	<i>Egria</i>	<i>Laminaria</i>	<i>Eisenia</i>	<i>Pterygophora</i>	<i>Cystoseira</i>	<i>Gigartina</i>
1	91	63	97	51	60	1	96
2	72	50	83	70	79	10	81
3	62	28	88	87	65	2	49
4	84	30	14	11	8	0	20
5	73	43	31	3	13	0	15
6	76	38	74	45	20	0	0
7	96	27	8	0	30	2	36
8	58	46	54	0	0	8	75
9	72	12	83	9	16	1	26
10	71	14	28	24	3	0	51
Mean	75.5	35.1	56.0	30.0	29.4	2.4	44.9

pect that preference orders would all tend to be similar among the grazing species examined. The consumption of some of the tougher algae (*Eisenia*, *Laminaria*, *Pterygophora*, *Gigartina*, *Cystoseira*) is greater than or equal to that of the relatively tender *Macrocystis* and *Egregia* in a sufficient number of cases to suggest that differential algal consumption could not be attributed solely to the degree of toughness of the algae. A more likely explanation of the observed results would involve selection of algal foods on the basis of chemical perception.

Assuming that food preference, as demonstrated in the laboratory, must indeed contribute to the behavior of grazing populations in the field, one might expect *Macrocystis* to receive concentrated grazing and to provide support for a great number of animals of at least these 11 species. Grazing is selective under certain conditions in the field (Leighton, 1964, Kelp Investigation, Final Report, in preparation). Selectivity disappears when grazing pressures become ex-

treme (Leighton, 1960:28). Although the food preference relationships found for the 11 benthic invertebrate species in the present study cannot be said to restrict any species to a given association of algae, as has been shown for the intertidal periwinkle, *Littorina obtusata* (Bakker, 1959), the preponderance of first choices falls under the headings *Macrocystis* and *Egregia*. In field studies some herbivores have appeared collectively oriented toward these plants and away from *Pterygophora* and *Cystoseira* (Leighton, 1964). A tendency may exist, therefore, for the grazing species to remain in *Macrocystis* and *Egregia* stands and, perhaps, to move into such stands from locations nearby which are less attractive with respect to food.³ The attractiveness

³ Experiments reported elsewhere (North, 1963), indicating the food value of *Macrocystis* as compared with other algae (*Egregia*, *Pterygophora*, and *Bossiella* sp.) based on conversion efficiencies, place the former in a leading position as a food plant for *Strongylocentrotus purpuratus* and *S. franciscanus*.

TABLE 3
DECIGRAMS OF DIFFERENT ALGAE CONSUMED BY 10 ADULT *Lytechinus anamesus*
IN 24-HOUR EXPERIMENTAL PERIODS*

EXPERIMENT	<i>Macrocystis</i>	<i>Egregia</i>	<i>Laminaria</i>	<i>Eisenia</i>	<i>Pterygophora</i>	<i>Cystoseira</i>	<i>Gigartina</i>
<i>Lytechinus</i> from La Jolla Submarine Canyon; depth 20 m; bottom sand							
1	51	0	25	3	1	7	54
2	31	9	17	4	0	0	65
3	25	3	12	0	0	0	39
4	14	10	0	0	0	0	24
5	22	3	0	0	0	0	14
Mean	28.6	5.0	10.8	1.4	0.2	1.4	39.2
<i>Lytechinus</i> from channel of Mission Bay; depth 2-3 m; bottom sand							
6	39	0	8	0	0	0	39
7	50	9	9	12	6	10	35
8	50	2	55	7	6	6	99
9	15	8	9	18	18	3	64
10	19	6	0	0	1	11	63
Mean	34.6	5.0	16.2	7.4	6.2	6.0	60.0

* Results are given for groups collected from depths of 20 m and 2 m in different locations.

TABLE 4
SYNOPSIS OF PREFERENCE ORDER RANKINGS

GRAZING SPECIES	<i>Macrocystis</i>	<i>Egregia</i>	<i>Laminaria</i>	<i>Eisenia</i>	<i>Pterygophora</i>	<i>Cystoseira</i>	<i>Gigartina</i>
<i>Aplysia</i>	2	1	6	4	5	7	3
<i>Astraea</i>	1	3	4	5	7	6	2
<i>H. corrugata</i>	1	2	4	3	5	6	7
<i>H. fulgens</i>	2	1	3	4	6	7	5
<i>H. rufescens</i>	1	2	3	4	6	7	5
<i>Lytechinus</i>	2	4	3	5	7	6	1
<i>Norrisia</i>	3	1	2	5	4	7	6
<i>Pugettia</i>	1	2	4	6	3	5	7
<i>S. franciscanus</i>	1	6	3	4	5	7	2
<i>S. purpuratus</i>	1	4	2	5	6	7	3
<i>Taliepus</i>	1	2	3	5	4	6	7
Total ($W_t^* = 0.61$)	16	28	37	50	58	71	48

* W_t = Coefficient of concordance for mean preference orders of all grazing species (see text); the value is significant at better than the 0.1% level.

of *Macrocystis* to its grazing species may help to explain why that alga in the field is often the center of grazing attack and why kelp beds hold the numbers and variety of grazers observed.

ACKNOWLEDGMENTS

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An Anatomical Study of the Hawaiian Fern *Adenophorus sarmentosus*¹

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THE ENDEMIC HAWAIIAN FERN, *Adenophorus sarmentosus* (Brack.) K. A. Wilson, occurs on all of the major islands, growing on moss-covered trees and occasionally also on mossy rocks. As a representative of the large but poorly understood fern family Grammitidaceae, *A. sarmentosus* was chosen for anatomical studies in order to contribute some information on the family which may be of value in later systematic studies of the group. Anatomical or morphological studies of the grammitids are rare. A series of recent papers by Nozu (1958-1960) presents the only anatomical investigation of members of this family except for a few notes published earlier by Ogura (1938).

The plant material used was collected at Wai-anae Iki on the island of Oahu in 1954 by Earl T. Ozaki. A voucher specimen has been deposited in the herbarium of San Fernando Valley State College. The fern was killed and fixed in F.A.A.; sectioning was done according to standard paraffin techniques. Leaves were cleared by the sodium hydroxide technique (Foster, 1949) and stained in tannic acid and ferric chloride (Wilson, 1958).

OBSERVATIONS

The rhizome of *A. sarmentosus* is erect or ascending, short, usually less than 1 cm in length, 0.5-1 mm thick, and clothed in reddish-brown, concolorous, linear-lanceolate scales (Fig. 1, 8). The roots are wiry, dark brown, and few-branched, often bearing propagules which develop into new plants (Fig. 1, 2). This vege-

tative means of propagation is known not only in *A. sarmentosus*, but also in the closely related *A. baalilioanus*, and should be looked for in the rare *A. pinnatifidus*. Similar reproductive behavior has been reported recently in *Asplenium plenum* of Florida (Wagner, 1963).

The petioles are short, less than 2 cm long, crowded on the rhizome, and bearing simple or branched deciduous, reddish-brown hairs. The blades are pinnatifid, elliptic-lanceolate, 8-15 cm long, 1-2.5 cm wide, and narrowing gradually at both ends, often becoming prolonged into a long caudate apex (Fig. 1, 3). The venation is pinnate, with free simple (rarely branched) veins with clavate or punctiform ends which do not extend to the margins of the blade (Figs. 1, 3 and 4).

The outline of the stem is almost a perfect circle in cross-section. The vascular cylinder is protostelic in the young stages and becomes solenostelic in older portions of the rhizome. During the transition from the protostele, a parenchymatous pith develops (Fig. 2, 1), within which a central phloem strand differentiates in slightly later stages (Figs. 2, 2 and 3). In the older portions of the stem the inner phloem of the solenostele is cylindrical and surrounds a central pith (Figs. 2, 13-17). The single leaf traces which arise from the main stele and lead to the leaves are surrounded by the sclerenchyma of the cortex which extends into the petiole itself. Each leaf trace is generally associated with two root traces which arise either below the juncture of the leaf trace with the stelar gap (Figs. 2, 2-5) or somewhat above this level (Figs. 2, 7, 29, 30). One instance was observed in which a leaf gap was associated with only a single root trace which arose directly opposite the gap rather than perpendicular to the plane of the gap (Fig. 2, 21). Not all roots, however, arise in association with leaf traces. Pairs of root traces were observed departing from the main stele in regions between

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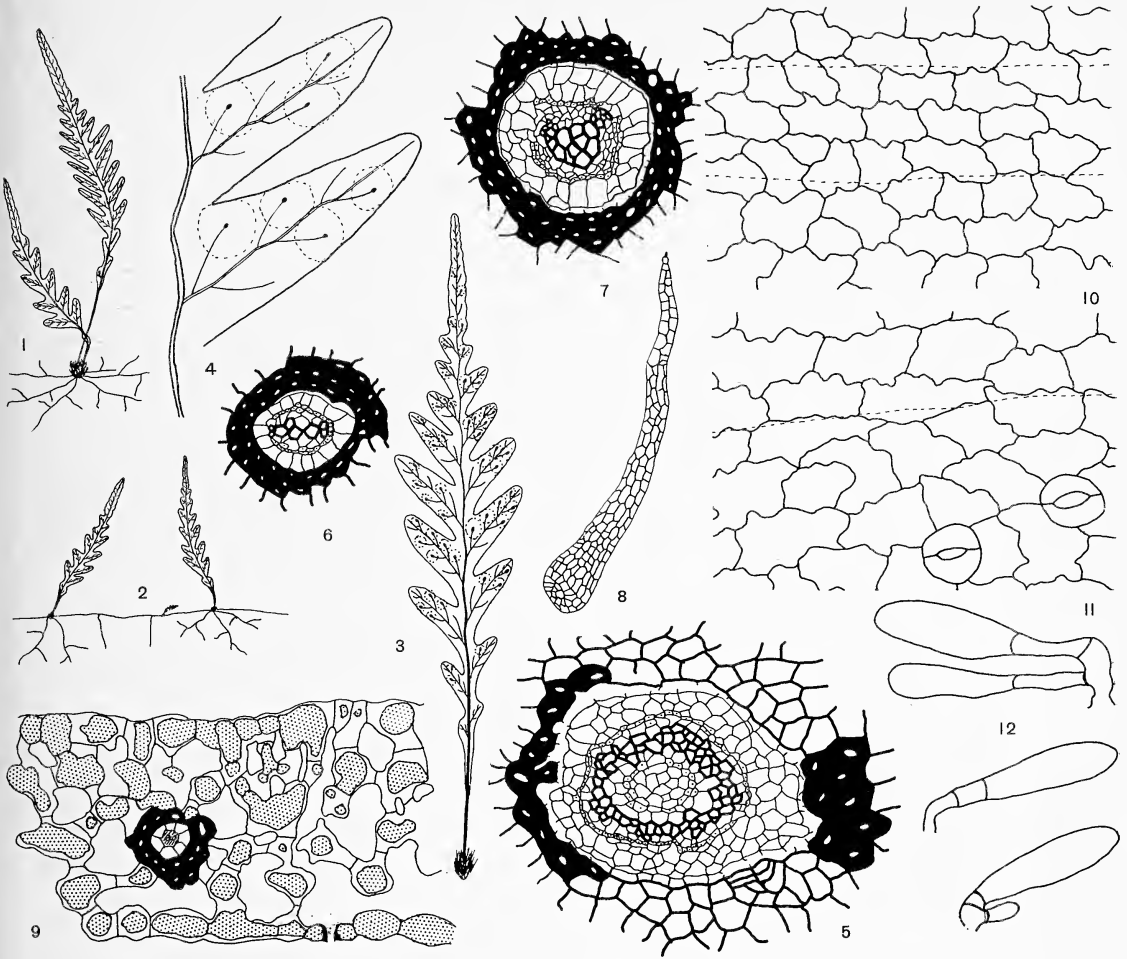


FIG. 1. *Adenophorus sarmentosus*. 1, Habit $\times \frac{1}{3}$; 2, habit showing vegetative reproduction by root propagules, $\times \frac{1}{3}$; 3, frond, $\times \frac{2}{3}$; 4, portion of frond showing venation, $\times 3\frac{1}{2}$; 5, cross-section of stele of rhizome $\times 100$; 6, cross-section of stele of root, $\times 100$; 7, cross-section of stele of petiole, $\times 100$; 8, rhizome scale, $\times 17$; 9, cross-section of lamina, $\times 100$ (stippled portions indicate cut surfaces); 10, upper epidermal cells, $\times 100$; 11, lower epidermal cells, $\times 100$; 12, epidermal hairs, $\times 100$.

successive leaf traces, showing no particular relation with the vascular supply to the leaf (Figs. 2, 13–16). The orientation of the root traces is horizontal as they arise from the stele as well as during their course through the cortex. The leaf gaps do not become closed in all cases before the departure of the next leaf trace. In our material the gap was observed to close in the lower portion of the rhizome (Figs. 2, 10–12), while in the upper portions no such closure was observed (Figs. 2, 19–31).

The stele is surrounded by an endodermis composed of small, thin-walled cells with con-

spicuous, bright-staining Casparian strips on the radial walls. In all of our material the stele is pulled away from the outer tissues of the stem at the region of the endodermis (Fig. 1, 5). This separation results in the destruction of most of the endodermal cells and apparently is caused by the differential action of killing and fixing agents on the tissues of the stele *versus* the surrounding cortical tissues.

The cortex is composed of 10–12 layers of cells. The cells of the innermost 5–7 layers consist of heavily thickened, often completely occluded, sclerenchyma cells. However, patches

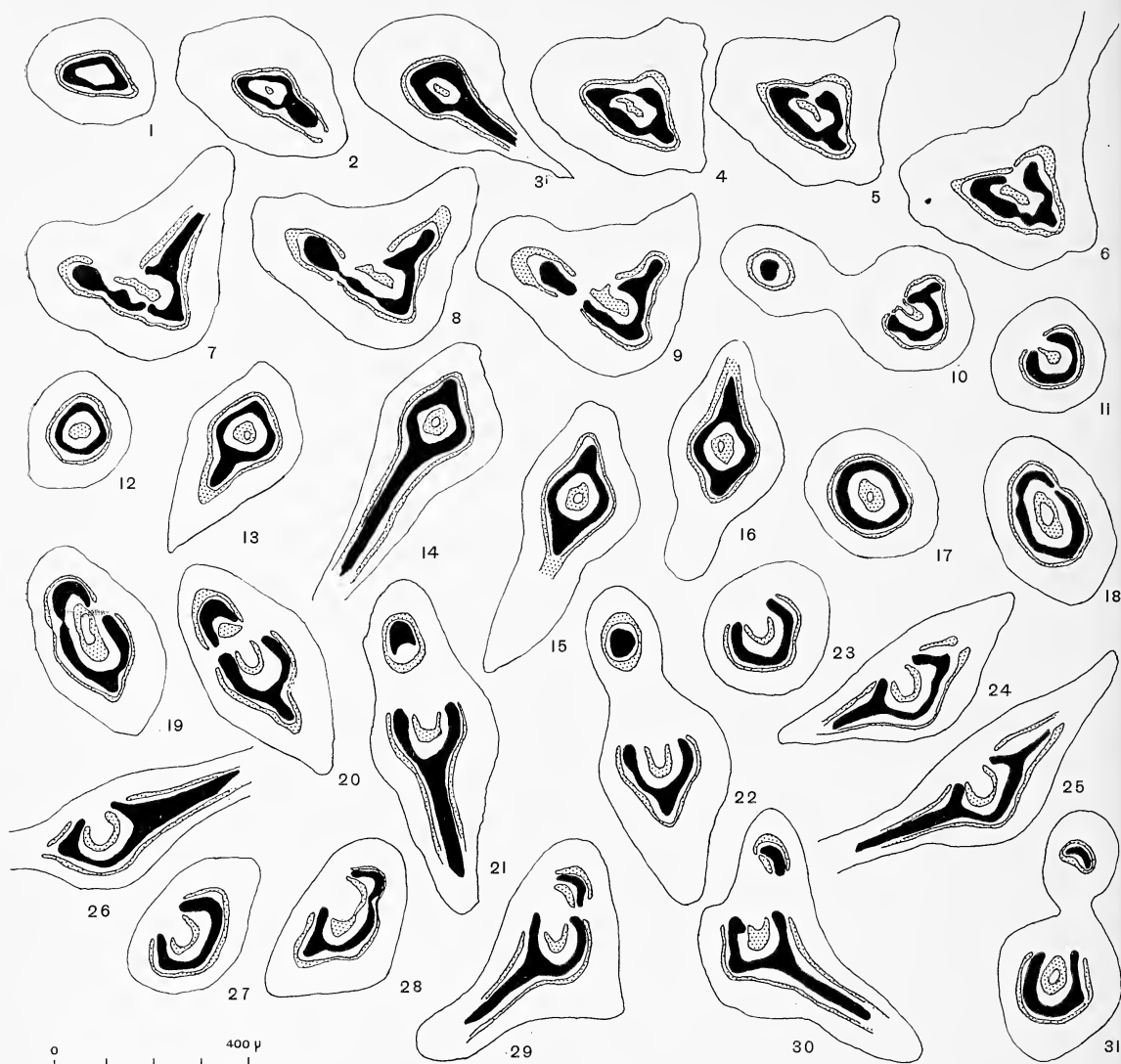


FIG. 2. *Adenophorus sarmentosus*. 1-31, Selected serial cross-sections of the stele of the rhizome showing origin of leaf traces and root traces.

of slightly thinner-walled, protoplast-containing cells often occur, usually directly opposite a departing leaf trace. The outer 2 or 3 cortical cell layers are composed of uniformly large parenchyma cells. The cells of the single-rowed epidermis are thin-walled.

The xylem cylinder is from one to three cells thick. Its tracheids are of relatively uniform size. The protoxylem tracheids are only about $\frac{1}{2}$ the diameter of the average metaxylem elements and are grouped in more or less distinct-

tive areas on the outer margin of the xylem cylinder. The xylem, therefore, is apparently exarch. Within the cylinder of xylem, the cells of the one-layered or occasionally two-layered internal phloem are separated in most instances from the xylem by a layer of parenchyma cells similar in structure to the cells of the central pith. Another layer of parenchyma also occurs between the xylem and the outer phloem. The cells of the outer phloem are conspicuously smaller than those of the inner phloem and

have a diameter of only $\frac{1}{2}$ – $\frac{1}{3}$ of the average of the elements of the inner phloem. In the outermost tissue of the stele, outside the narrow strip of outer phloem, occur the numerous large cells of the pericycle (Fig. 1, 5).

The stele of the petiole is circular in cross section and is surrounded by flat endodermal cells which separate it from the heavily sclerified layers of the cortex. The center part of the stele is occupied by the single xylem strand which, in cross section, is roughly reniform (Fig. 1, 7). The protoxylem elements are in groups of about six at each of two points forming the adaxial lobes of the strand. The xylem is separated from the phloem by two or three layers of irregularly shaped, nucleated parenchyma cells. The phloem area is made up of one or two rows of tiny, thin-walled cells, and surrounds the entire xylem core except at its protoxylem poles. Between the phloem and the endodermis occur the large, nucleated, thin-walled cells of the pericycle containing plastids. The cortex is clearly differentiated from the epidermis and is composed of six to eight layers of thick-walled sclerenchyma cells. The thickness of the cell walls of the cortical cells increases gradually, so that the cells in the outermost layer have extremely thick walls. There is also a gradual decrease in the diameter of the cells toward the periphery of the cortex. The large thin-walled cells of the epidermis are subtended by a layer of slightly smaller thin-walled cells containing numerous plastids which separate the cortical sclerenchyma from the epidermis itself. In the lateral marginal wings of the petiole the epidermis, containing occasional pairs of guard cells, is subtended by a tissue of loosely arranged parenchyma cells with large intercellular spaces.

The adaxial laminar surface lacks stomata. In face view the epidermal cells are approximately 1–3 times as long as wide, and their general outline is somewhat oblong. The longitudinal walls are moderately wavy (Fig. 1, 10). The abaxial laminar surface is characterized by more irregular cells, generally with pronounced undulate walls (Fig. 1, 11). Both epidermal surfaces bear scattered suberect or erect hairs. The epidermal hairs are two- to

four-celled, uniseriate, simple or frequently branched, and with a large, reddish-brown terminal cell (Fig. 1, 12).

In cross section, the cells of the upper epidermis are seen to have irregular vertical projections which reach below the epidermal layer itself and come in contact with the spongy tissue of the leaf (Fig. 1, 9). The lower epidermal cells rarely display such projections. The mesophyll is composed entirely of irregular, loosely arranged, spongy parenchyma cells with large intercellular spaces. The round sori are borne terminally on the veins. The sporangia have a single row of cells at the base of the stalk, and an annulus with 11–13 thickened bow cells (Wilson, 1959a). The spores are green, tetrahedral, trilete, without exospore, and have an average measurement of $34 \times 12 \mu$ (Selling, 1946).

The roots have a diarch stele with two protoxylem groups, one at each end of the xylem tract (Fig. 1, 6). The one- or two-layered phloem surrounds the xylem except at the protoxylem poles, and is separated from it by a layer of parenchyma cells. The endodermal cells are small, and thin-walled, and were difficult to observe in our preparations. This many-celled endodermis is surrounded by the inner layer of the two layers of heavily sclerified cortical cells. The outer two or three layers of cortical cells are conspicuously thinner-walled.

DISCUSSION

In general, the structure of *Adenophorus sarmentosus* agrees with the observations of Nozu (1958–1960) made on species of *Micropolypodium* (*Xiphopteris*), *Scleroglossum*, and *Grammitis*. On the basis of these studies and of general systematic surveys (Holtum, 1954; Copeland, 1947), the solenostele of *A. sarmentosus* seems to be characteristic of the rhizome of most of the Grammitidaceae, although in some groups a dissected solenostele is not uncommon. The absence of an internal phloem in the younger portions of the rhizome of *Adenophorus sarmentosus* is noteworthy. A similar medullated protostele was described in *Micropolypodium okuboi* by Nozu. The stele of *A. sarmentosus*, however, soon becomes soleno-

stelic, interrupted occasionally by leaf gaps. In this it resembles the species of *Grammitis* investigated by Nozu. The dictyostelic vascular cylinder which he reported for *Scleroglossum pusillum* evidently is not repeated in *A. sarmentosus*. However, the failure of some leaf gaps to close may perhaps be interpreted as a trend towards the further dissection of the solenostele. Conclusive evidence cannot be presented at this time to establish the evolutionary trend in the vascular structure of the rhizome in this family. The hypothesis that the family consists of a reduction series seems to us to be most acceptable. With this point of view, we would interpret the solenostele as having been derived from a dictyostele, although it seems probable that some dictyostelic grammitid groups in turn have evolved secondarily from solenostelic ancestors. The temptation to make broad generalization about evolutionary trends is one to which we would rather not yield until more comparative data are available.

A leaf supplied by a single vascular trace with a U- or V-shaped xylem in the petiole seems to typify members of this group. Ogura (1938) designated this particular type of petiolar vascular structure as the "Grammitis" type and subsequent investigators have found similar patterns in other grammitids (Holtum, 1947; Nozu, 1958-1960). The xylem strand of *A. sarmentosus* adds still another species to this list.

It is difficult to attempt to interpret the phylogenetic relationship of the Grammitidaceae on the basis of anatomical investigations of so few members of the group. Numerous studies have been published which indicate that these ferns represent a natural group. Other than anatomical studies of the sporophyte, evidence from the gametophyte generation (Stokey, 1959; Stokey and Atkinson, 1958) and from the morphology of the sporangium (Wilson, 1959a; 1959b) strongly support the distinctness of the family. Broad phylogenetic conjectures would best await additional studies within the Grammitidaceae. Systematic problems within the family will also require detailed studies before a satisfactory taxonomic arrangement can be proposed. Some of these problems have been discussed recently for the genus *Adenophorus*

by Wilson (1964). We have undertaken this present study in order to obtain some information which may be of value in later systematic considerations of the grammitid ferns. Other similar studies are badly needed.

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Desilication of Halloysite and Its Relation to Gibbsite Formation¹

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ABSTRACT: The evidence presented points to the alteration of halloysite to gibbsite. Mineralogical data, as determined by X-ray and differential analysis, verify identification of halloysite and gibbsite. Chemical data confirm the expected lower silica and higher alumina content for samples which are predominantly gibbsitic. It is reasonable to assume from petrographic evidence that gibbsite develops by desilication of halloysite. Halloysite amygdules undergo desilication along the outer peripheries, where acid silica-deficient waters pass, attacking the halloysite by dissolving silica. Halloysite is stable only if it is protected from such solutions, or if the solution passing by is saturated with silica.

Whereas alteration of feldspar to halloysite involves a gain in volume, a loss in volume follows desilication of halloysite. This loss in volume is exemplified by the surface cracks clearly visible in the desilicated halloysite.

IN AN EARLIER PAPER Sherman and Ikawa (1959) described the occurrence of gibbsite amygdules in the Haiku bauxite area of Maui, Hawaii. At that time it was proposed that gibbsite amygdules formed in rock vesicles by rhythmic precipitation of hydrated alumina. Subsequent and more thorough investigation of the same area and elsewhere in the Hawaiian Islands suggests a more complex sequence of events in the development of these gibbsite amygdules. In this paper the results of field and laboratory studies are presented to explain halloysite formation and its subsequent desilication to gibbsite.

Bates (1962) suggested that gibbsite is produced in Hawaii by (1) removal of silica from halloysite, (2) dehydration of aluminum gel, and (3) precipitation from solution. The first mode of formation is of primary interest in this study.

FIELD DESCRIPTION

All data presented in this work are for samples collected from the Haiku bauxite area described

by Sherman and Ikawa (1959). Similar features have been observed on the islands of Hawaii, Molokai, Oahu, and Kauai, but the Haiku site represents the most extensive halloysite-gibbsite deposit of this kind. This site is located approximately 2 miles east of Pauwela Village, Maui, and can best be studied along deep roadcuts on the highway leading to Hana.

The soil occurring in this area is mapped as the Pauwela series of the Humic Ferruginous Latosol. Soils of the Pauwela series are found on the island of Maui from sea level to 1,500 ft elevations in areas receiving an annual rainfall of 80–150 inches.

Highly vesicular andesitic pahoehoe probably constituted the parent rock. Pahoehoe lavas are often vesicular and have a rather regular distribution of vesicles; some are cellular to a degree that makes them nearly pumiceous, so that when these vesicles are filled with secondary minerals a larger volume of the rock may be occupied by them.

A description of the Pauwela soil can be found in Cline et al. (1939). Approximately 3–5 ft below the surface there appears a yellowish-brown weathered rock (saprolite) retaining much of the original rock structure. In the area investigated this weathered zone persists even in the deepest portion exposed by the roadcut, although occasional unweathered cores also may be seen.

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FIG. 1. Fragments of halloysitic veins from Haiku, Maui. Dark coatings are surface manganiferous deposits. Scale units in mm.



FIG. 2. Halloysitic amygdules from Haiku, Maui. Note relatively smooth surface. Scale units in mm.

Closer examination of the saprolytic material reveals numerous milky-white, spherical bodies (Figs. 2, 3). In distribution and dimension they appear to be vesicle fillings, and henceforth will be referred to as amygdules. Similarly, joints and crevices in the rock have become filled with this material (Fig. 1) and appear as veins. Differential dispersion of the matrix by rain, and protrusion of amygdules and veins give these features exaggerated prominence. In selected hand specimens, however, as much as 50–75% of the volume may be occupied by these amygdules.

RESULTS

Halloysite and gibbsite were identified as the two important crystalline minerals in the amygdules and veins by X-ray diffraction analyses. Halloysite was in the form of the fully hydrated ($4\text{H}_2\text{O}$) form, indicated by the appearance of the 10 \AA ($8.8^\circ 2\theta$) spacing.

Figure 4 shows the X-ray diffraction diagrams of the veins and amygdules ranging in mineralogy from essentially pure halloysite to pure gibbsite.

Table 1 gives the chemical composition of these same samples. Halloysite is normally given the formula $2\text{SiO}_2 \cdot \text{Al}_2\text{O}_3 \cdot 4\text{H}_2\text{O}$ and, therefore, should have a mole $\text{SiO}_2/\text{Al}_2\text{O}_3$ ratio of 2. The values given in Table 1 are all less than the theoretical value of 2. This is understandable since both the X-ray and differential thermal data (Fig. 5) show traces of gibbsite even in the predominantly halloysitic samples. Even when no gibbsite can be detected, Hawaiian halloysites, in general, never attain a $\text{SiO}_2/\text{Al}_2\text{O}_3$ ratio of 2 (Nakamura and Sherman, 1963).

Pure gibbsite should be free of silica, but the sample containing the largest quantity of gibbsite still retains 6.55% SiO_2 . The 02 (hk) reflection for halloysite which appears at $20^\circ 2\theta$ in the X-ray diagram is masked by a major

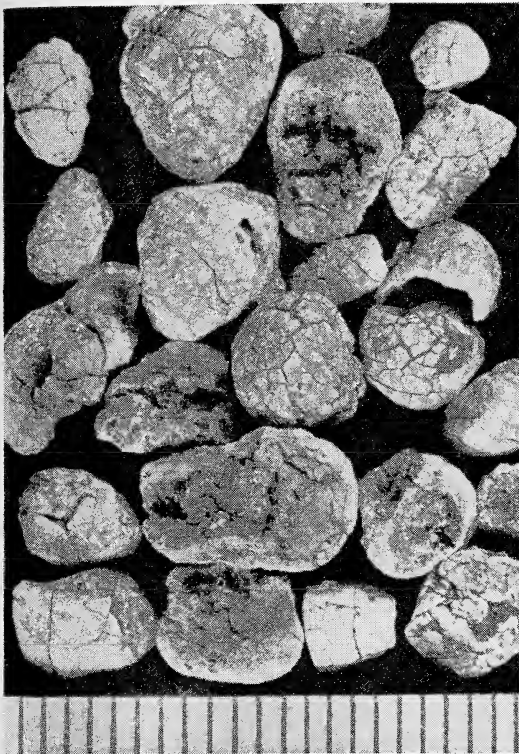


FIG. 3. Gibbsite or desilicated halloysite. Note characteristic cracked surface. Scale units in mm.

gibbsite line, and detection of trace amounts of halloysite by this method in the presence of gibbsite is difficult at best. Differential thermal analysis of this sample, however, confirms identification of halloysite by the 550°–600° endotherm characteristic of halloysite which appears in all four samples.

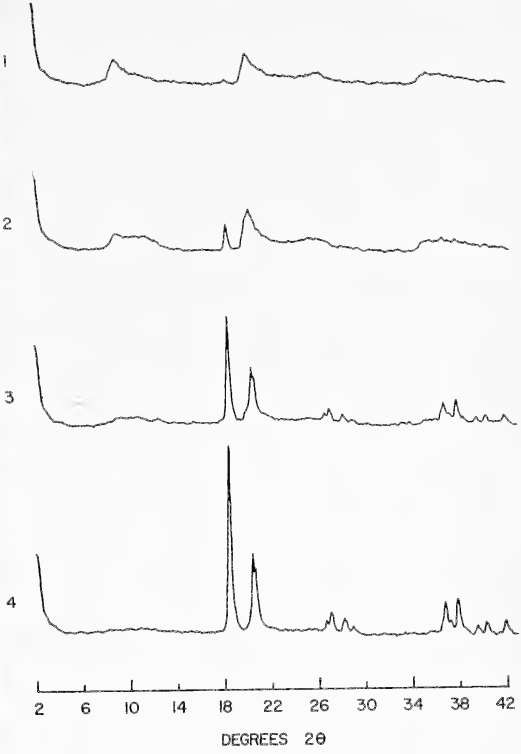


FIG. 4. X-ray diffraction (nickel-filtered, copper K α radiation) diagram of veins (sample 1) and amygdules (samples 2–4) from Haiku, Maui.

Examination of thin sections merely confirmed the X-ray and thermal data, but clarified the genetic relation of gibbsite to halloysite. Figure 6 shows a vesicle nearly filled with halloysite. The matrix feldspar has also been altered to this mineral and there is no evidence for gibbsite.

TABLE 1
CHEMICAL COMPOSITION (IN %) OF VEINS (SAMPLE 1) AND AMYGDULES (SAMPLES 2–4) FROM HAIKU, MAUI, SHOWING RANGE IN SILICA-ALUMINA RATIO

SAMPLE NO. (as in Figs. 4, 5)	SiO ₂	Al ₂ O ₃	Fe ₂ O ₃	TiO ₂	MnO	L.O.I.	SiO ₂ /Al ₂ O ₃
1	39.42	40.58	5.55	1.40	0.13	23.85	1.649
2	36.83	44.32	2.11	0.44	0.03	16.39	1.410
3	15.29	57.33	4.30	0.48	0.08	23.85	0.453
4	6.55	64.14	1.41	0.44	0.02	28.07	0.173

Figure 7 is a photomicrograph corresponding to sample 3 in the X-ray, thermal, and chemical data. All data point to a mixture of halloysite and gibbsite. A thin section, however, shows that the gibbsite exists on the outer periphery of the

amygdules and not as an intimate mixture with halloysite.

Figure 8 represents a thin section of a thoroughly gibbsitized amygdule. Although these are not evident in Figure 8, most gibbsite amygdules are characterized by surface fractures. Figure 3 clearly shows this feature; in Figure 2 the amygdules composed predominantly of halloysite fail to show this.

DISCUSSION

It is often difficult to distinguish halloysite from gibbsite in hand specimen. Therefore, X-ray, differential thermal, or chemical analyses are often necessary to confirm the identification. Differential thermal analysis is probably the best method for making quantitative estimates of these two constituents.

Once the minerals have been identified, op-

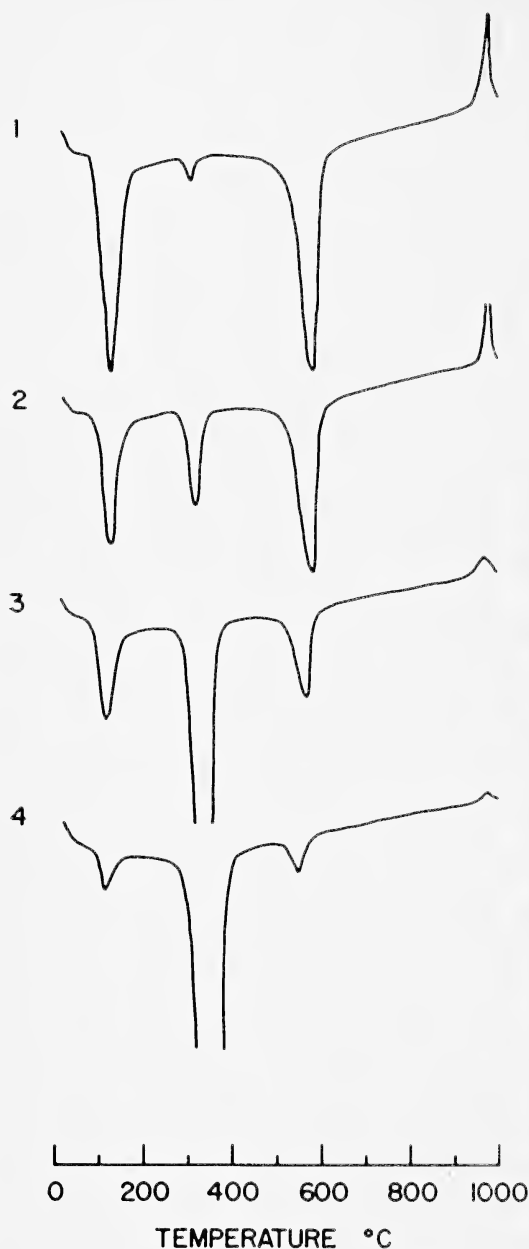


FIG. 5. Differential thermal diagrams of veins (sample 1) and amygdules (samples 2-4) from Haiku, Maui.

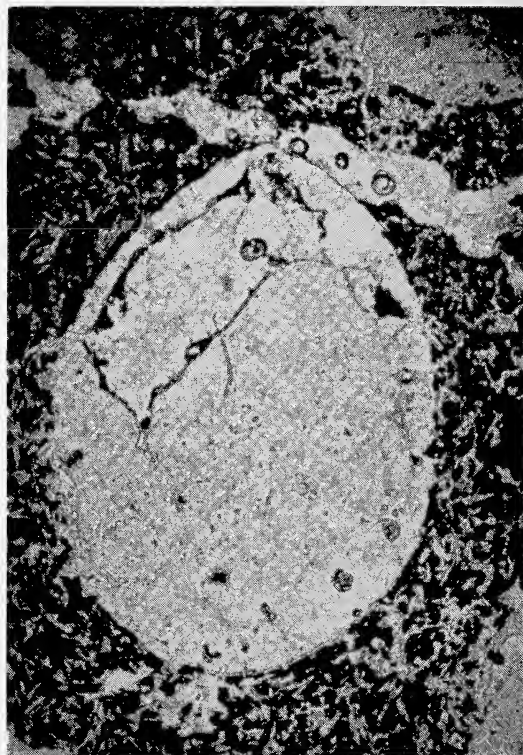


FIG. 6. Vesicle nearly filled with halloysite. Dark areas are residual grains of iron ore; clear areas in surrounding matrix are halloysite clays pseudomorph after feldspar. Plain light, $\times 320$.



FIG. 7. Isotropic halloysite desilicating to birefringent gibbsite along periphery of amygdale. Crossed nicols, $\times 320$.



FIG. 8. Completely gibbsitized amygdale. Dark area represents opaque iron oxide and pore space. Crossed nicols, $\times 320$.

tical methods can give insight to the relationship of these minerals to one another by their arrangement and distribution in a specimen. Thin-section studies suggest that halloysite and gibbsite are not necessarily synthesized independently of each other, but follow a predictable pattern of formation.

The source of silica and alumina for synthesis of halloysite is mainly in the feldspars. In the feldspars the aluminum ion, as well as the silicon ion, is tetrahedrally coordinated. Each tetrahedrally coordinated aluminum substituted in the three-dimensional silica network imparts to it a negative charge, which is satisfied by either sodium or calcium. Halloysite, on the other hand, consists of a sheet of tetrahedrally coordinated silica joined to an octahedrally coordinated alumina sheet through common oxygen linkages.

When a feldspar is altered directly to halloysite, forming pseudomorphs after feldspars, neither hydrated silica nor alumina need move more than a few atomic diameters to recrystal-

lize in the form of halloysite. Nevertheless, all the sodium and calcium, and a considerable portion of the silica must be removed from the volume occupied by the feldspar to accommodate the new mineral. Water incorporated into the crystal lattice of halloysite more than makes up for loss of the metallic cation and silica.

Implicit in the assumption that halloysite precipitates in vesicles is the movement of alumina into these voids. Alumina probably moves early in the weathering of the rock as the anion $\text{Al}(\text{OH})_4^-$, when the sodium ion concentration is still relatively high. In an acid environment the tetrahedrally coordinated anion is incorporated octahedrally into the halloysite lattice. Since the tetrahedrally coordinated alumina can be stabilized in acid media by silica (Iler, 1955), it is not unlikely that octahedral alumina sheet is the nucleus to which the silica sheet is joined. In systems retaining sodium and calcium, the secondary mineral is a zeolite rather than

halloysite. There is evidence in certain Hawaiian soils that zeolites do in fact weather to halloysite.

Bates et al. (1950) long ago proved the morphology of halloysite to be tubular; Hawaiian halloysites (Nakamura and Sherman, 1963) are often more closely related morphologically to the spheroidal, Japanese allophanes described by Sudo and Takahashi (1955). Critical electron microscope examination of Hawaiian halloysites should be extremely interesting.

One might expect the gibbsite content to increase with increasing proximity to the soil surface. However, samples 4, 3, 2, and 1, showing increasing halloysite content in the order given, were obtained at approximately equal depths below the surface. Mineralogical variability can be readily explained on the basis of certain weathering factors.

The gibbsite content in any unit volume of the weathering profile depends on a number of factors. In general, the gibbsite content increases with increasing proximity to the soil surface, where weathering is most intense. However, even at depths quite distant from the surface, zones exist which are highly gibbsitic by virtue of their proximity to an internal drainage channel. All other factors being equal, the permeability of the rock also controls rate of weathering.

In general, any differential volume undergoing weathering may be treated as an open system. Two distinct volumes might be given special consideration here: (1) the volume occupied by a feldspar crystal, and (2) the voids or vesicles. From the moment atmospheric pressure and temperatures are attained, the feldspar is subject to decomposition by CO_2 -saturated leaching waters. If the feldspar occurs near the surface of a lava flow, the CO_2 concentration is high and the reaction will be relatively rapid. At greater depths, the leaching solution is saturated with silica, alumina, sodium, and calcium, and is depleted of CO_2 . This saturated solution accumulates in voids, and precipitates in the form of an appropriate secondary mineral.

The rate at which this process takes place will depend on the amount of water passing through this unit volume. In an open system, the difference between the concentration of the outgoing and of the incoming solution gives a measure of the weathering rate. In an open system, a void in the rock gains constituents early in its history; but, in the final stages of weathering, even this volume suffers loss of certain material. Gibbsite as a final weathering product is extremely stable and will resist further decomposition; thus, it accumulates to form some of the world's bauxite deposits.

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The Rise of Sea Level in Contemporary Times at Honaunau, Kona, Hawaii¹

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ABSTRACT: Bait cups, net-tanning tubs, and playing boards for the checker-like game of *konani*, which were hollowed out by the ancient Hawaiians on the surface of pahoe-hoe lava flows a short distance above sea level at the City of Refuge, Honaunau, Hawaii, are now submerged and unusable for their original purpose. Increased depth of water over the traditional land route used in approaching the place of refuge, comparisons of old and new photographs, and increasing storm damage to structures, also indicate a relative sinking of the shore, at a rate of about 1 ft per century. The sinking is endangering some of the structures, and imposes a special problem in the preservation of the area. Other evidence indicates sinking of other parts of the island of Hawaii, but by less definite amounts. The rate of change of relative level of land and sea at Honaunau is much greater than that of world-wide change of sea level, and must be the result of actual sinking of the island. The logical explanation lies in isostatic adjustment resulting from loading of the earth's crust by the great added mass of the volcanoes. The southern part of the island of Hawaii appears to be sinking isostatically at a rate of about 8 or 9 inches a century.

A BY-PRODUCT of recent archeological and historical investigations at the newly established City of Refuge National Historical Park at Honaunau, Kona, Hawaii (Fig. 1) is the discovery that the coastline is sinking. A continuation of this movement will endanger valuable prehistoric and historic structures in the Park and will bring about considerable changes in the coastline. Inasmuch as the goal of the National Park Service, U. S. Department of the Interior, is to restore the scene and selected structures of this ancient Hawaiian governmental and religious center to their appearance during the late 1700's, this threat may pose major problems to administrators of the area and restoration technicians during the next century.

The purpose of this paper is to document the rise of sea level within the last 200 years, to call attention to the problems that may arise as a result of the rise, and to suggest the probable geological explanation of the rise. The portion

of the paper dealing with historical and archeological evidence of the change is written by Apple; that dealing with geological aspects is by Macdonald.

HISTORIC AND ARCHEOLOGICAL FEATURES

It is immaterial to present and future administrators, charged with restoration and preservation of the land and structures, whether the land is sinking or the water is rising. The concern of administrators will be with the present and potential engulfment of the shore and its features, with attendant progressive changes in the location of the shoreline, as well as damages from storms and high seas in increasing areas and intensity.

Congress authorized the Park in 1955 and, after land acquisition, resident administration and establishment took place in 1961. The Park's purpose is to make its visitors understand and appreciate the history and culture of the ancient Hawaiians, and to recognize that the Hawaiian heritage is a part of the history and culture of the United States. The major interpretive theme of the Park is the concept and practice of refuge in the ancient Hawaiian civilization before 1819

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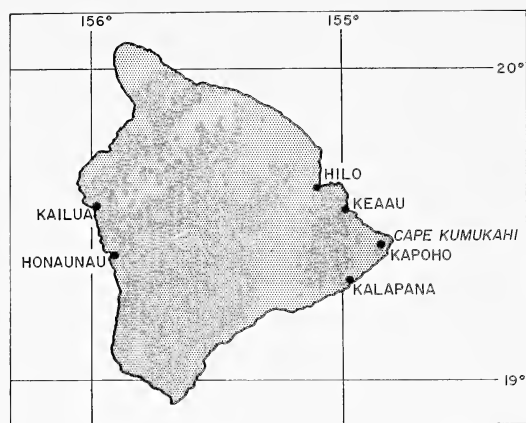


FIG. 1. Map of the island of Hawaii, showing localities referred to in text.

—a custom that so much resembled that of sanctuary in medieval Europe. Secondary interpretive themes are the rise of the Kamehameha dynasty; the transition of the Hawaiians in the Honaunau area to the present; and the Hawaiian uses of the land and sea, especially the tidal pools and adjacent offshore waters. The interpretive method is to exhibit the structures and land surfaces, restored as appropriate, which are associated with these themes. The numerous prehistoric and historic features of the area constitute exhibits-in-place.

Some of the coastal exhibits-in-place have been damaged or obliterated in whole or in part since 1823, when they were first accurately sketched, described, and/or measured by missionary William Ellis (1917:123–128). Many man-made coastal features, such as bait cups and net-tanning basins, are now under water except at extreme low tides. The shoreline of Ke-one-ele cove (Fig. 2) has receded in recent years, and has cut back into the coconut grove. These and other forms of creeping engulfment portend major problems for the future in preserving the prehistoric scene and structures, even as they produce less severe problems in the present. Among the important features threatened is the dry masonry platform of the temple, Hale-o-Keawe, which is in an extremely exposed position. The temple that once stood on this platform and is now scheduled for early restoration contained by 1818 the deified bones of at least 23 chiefs and kings, all of them male an-

cestors or relatives of Kamehameha the Great, including one of his sons (Barrere, 1957:70–80).

Just inland from the platform of the Hale-o-Keawe is Ke-one-ele cove, beleived to be the royal canoe landing used by Kamehameha the Great in 1782, when he arrived at Honaunau in his single canoe "Noiku" to conduct state religious ceremonies. Although it was not anticipated at the time, these ceremonies marked the beginning of Kamehameha's conquest of all the Hawaiian Islands and his founding of the historic Kingdom of Hawaii (Barrere, 1957:55–61; Ii, 1959:13). Photographs taken of the vicinity at Ke-one-ele cove in 1919 by members of the Bishop Museum staff show a rock rubble running between the sandy head of the cove and the platform of the Hale-o-Keawe (Bishop Museum negative 3436, by J. F. G. Stokes). A U. S. Army Air Corps aerial photograph taken January 24, 1925 (Bishop Museum negative B2829), and a panoramic photo by Ray Jerome Baker taken between 1921 and 1925, show this rubble transformed into a neat seawall, estimated to be 6 ft wide and 6 ft above the sea level at the time the picture was taken. The seawall was probably built in the period 1921–24 by the County of Hawaii during the early years of its administration of the City of Refuge as a County park (Emory, 1957:35). Probably there was a local tradition, or perhaps physical evidence, that the rubble once had been a seawall. This neat seawall was very short-lived. A photograph taken by the U. S. Army Air Corps on January 25, 1926 (Bishop Museum negative 2831), shows it reduced again to rubble.

The sandy head of Ke-one-ele cove has crept inland since the 1920's, and its movement to the south was watched during high seas on January 6, 1962 (a movement that has not been restored by the building phase of the normal beach cycle). A snapshot taken by the Reverend Albert S. Baker in 1926, and a panoramic photograph by Ray Jerome Baker (no relation) at about the same time show presently identifiable coconut trees. The present waterline is close to the base of one of the trees. In about 1926 the edge of the water was an estimated 20 ft away. The roots of this tree, which was young in the 1920's, were protected in January, 1962

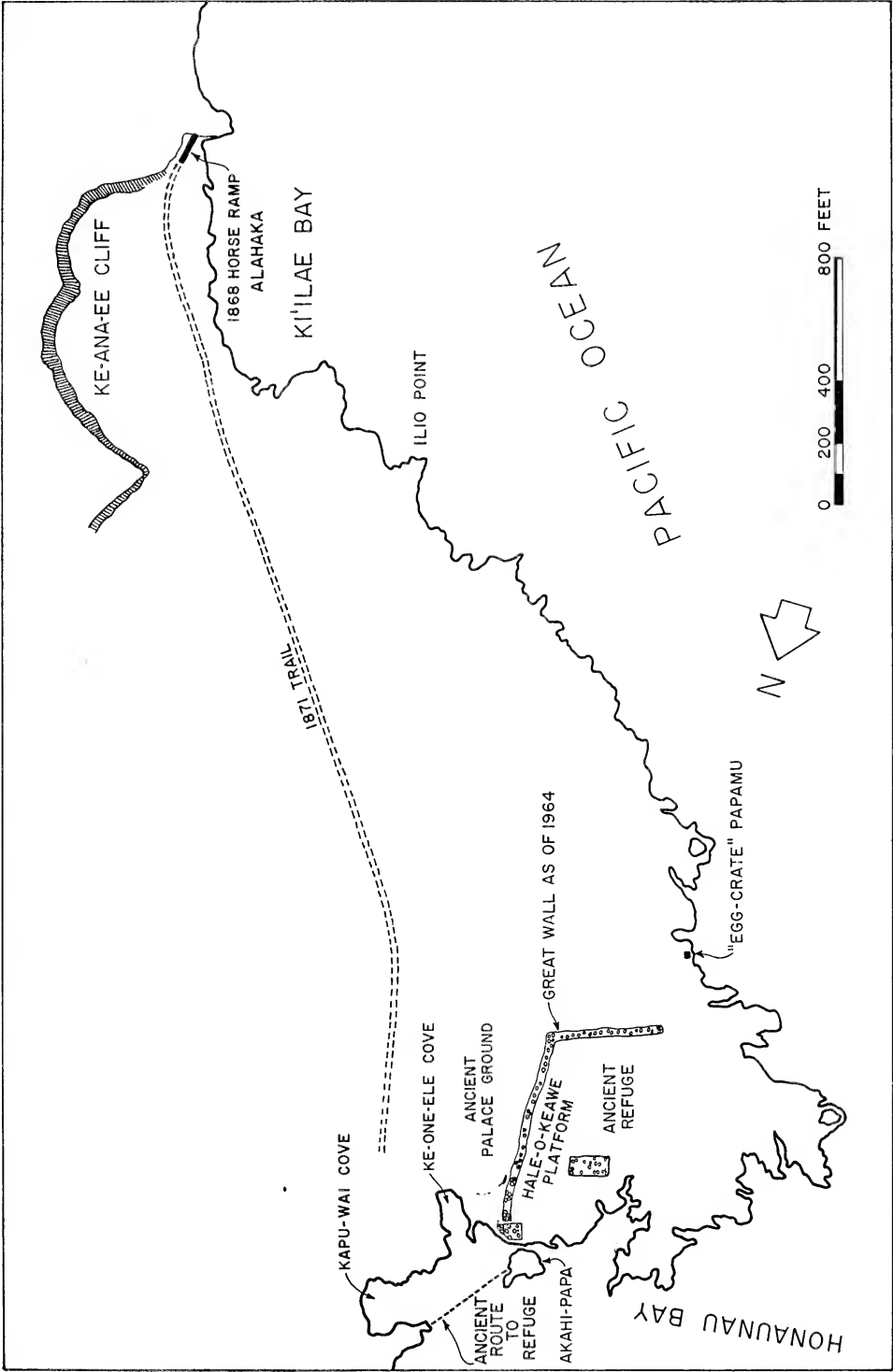


FIG. 2. Map of the Honaunau area, showing location of features referred to in text.

only through the quick construction of a rock retaining wall to halt washout by high seas that followed the storm on January 6. The tree is the larger one on the beach in the 1926 snapshot (Fig. 3), and the retaining wall built in 1962 is shown in a 1964 photograph (Fig. 4). On the basis of these photographs and personal conversations between Apple and Eli Carter, who was born and raised at Honaunau Bay and was the keeper of the former County park, we estimate the head of the cove has moved at least 20 feet inland since the early 1920's.

A series of photographs of a dry masonry ramp, built in 1868 to permit horses to pass along the coast up and down Ke-ana-e'e cliff (Fig. 2), indicates rapid deterioration of the ramp since 1950 (Apple, 1962: figs. 22-25).

Because of its exposed position in Ki'ilae Bay, the ramp is struck by waves during storms and high seas. Apparently the ramp stood almost intact from 1868 to 1950, but a displacement of rocks occurred on its seaward side near the top during the intense earthquake of August, 1951 (Macdonald and Wentworth, 1951). Subsequent sea action opened and widened the damaged area so that by 1963 passage over the ramp was dangerous. The National Park Service repaired the ramp in 1963, using concealed steel reinforcements and mortar because of the frequent high wave conditions. The earthquake damage in 1951 may have been the result of more frequent wetting and lubrication of the dry masonry by splash from waves. The rapid subsequent expansion of the damaged area was



FIG. 3. Head of Ke-one-ele cove, looking south, in 1926. The larger tree on the beach is the one referred to in Figure 4. (Snapshot by Rev. A. A. Baker, courtesy of Mrs. Burton J. Loucks. City of Refuge negative 846.)

certainly influenced by this frequent wetting during recent years. During the repair project workmen often were soaked with spray, but residents who had used the ramp in the early 1920's do not recall any spray at that time or any concern for damage to the ramp from high seas.⁴

The creeping erosion of the beach at Ke-one-ele cove and the recent damage to the 1868 horse ramp are modern events. There is also expert testimony and physical evidence that the water level at Honaunau was once lower than at present.

⁴ On-site interviews by Apple with Mrs. Mabel Kehi Alporque, April 6, 1963; with Moses Kalele, April 6, 1963; with William J. Paris, August 2, 1961; with Mrs. Martina Kaili Kekuewa Fuentevilla, July 28, 1961; and with Henry Hua, August 1, 1961.

After investigating the City of Refuge in 1919 and conducting numerous on-site interviews with long-time residents of the area, Bishop Museum anthropologist John F. G. Stokes reached the conclusion that a subsidence may have submerged certain features of ancient Hawaiian life (Stokes, 1957:199–212). Artificial concavities in the rocks which by 1919 Stokes (1957:199, 211) indicated were under water at high tide, are now exposed only at low tide. Some of the concavities are pictured in Figure 5.

Many of the artificial concavities in the lava are under water most of the time, and some are exposed only at extreme low tide. They were made by the metal-lacking prehistoric Hawaiians with hammer stones, or by abrasion with sand, stones, and pounders—a most arduous process.

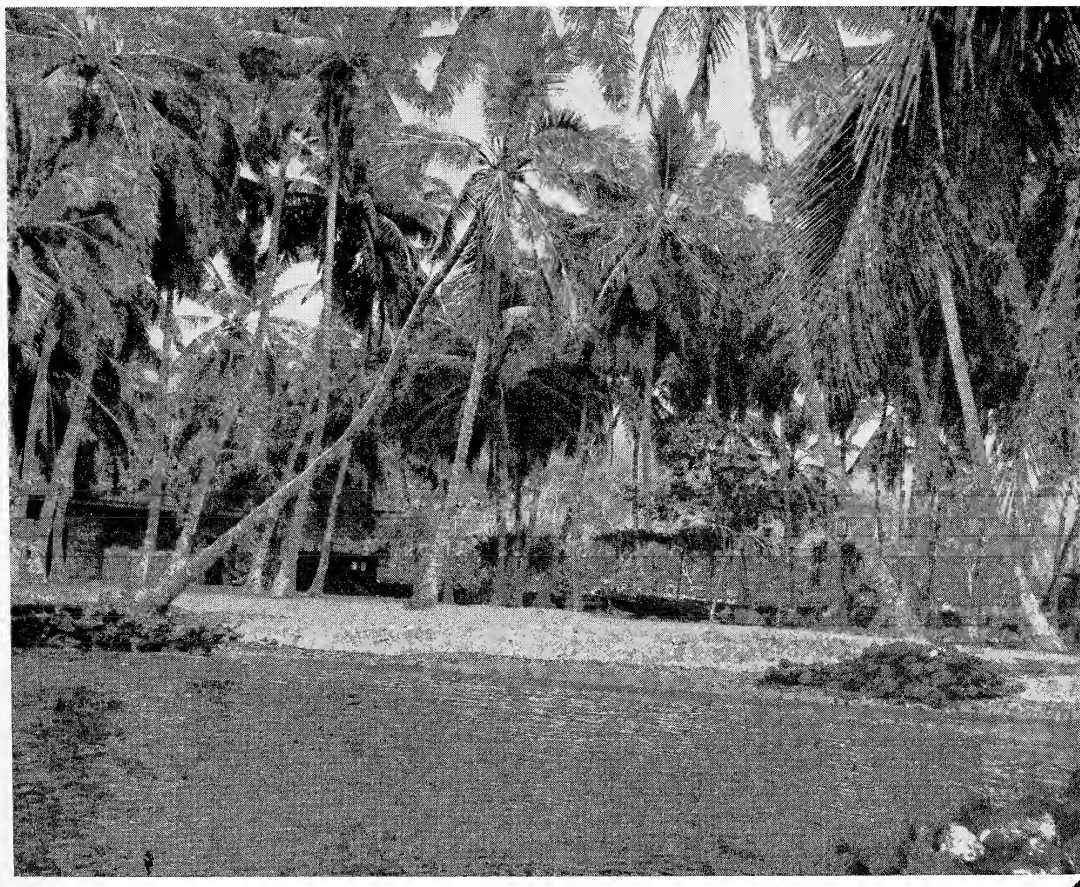


FIG. 4. Head of Ke-one-ele cove, looking south, in 1964. The base of the same coconut tree (left) shown in Figure 3 has been protected with a crude sea wall. (City of Refuge negative 1001.)

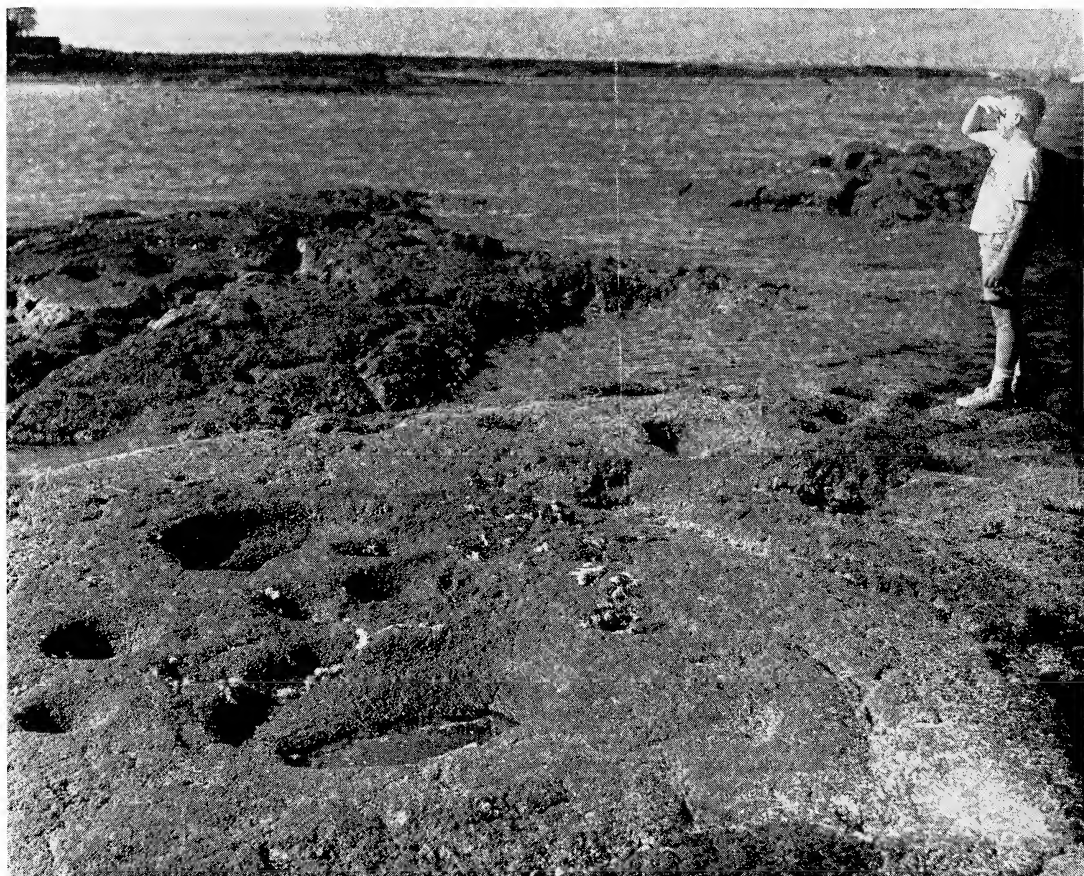


FIG. 5. Pu'u Ehu at low tide, November, 1963. This is the beginning of the ancient route through water to the refuge. The cups and basins still hold water left by the last high tide. (City of Refuge negative 1011.)

Their purposes at Honaunau Bay were described by Stokes (1957:199-200):

"Some are oval, about the size and shape of a baby's bath tub, and were used for tanning nets; others of smaller size are circular, and were mortars for pounding the tasty seaweeds; smaller ones yet were for pounding salt; while on the edge of the lava and overlooking the sea may be seen others, still smaller, for pounding crabs and sea-urchins as *hauna*, or chum to attract fish. . . . Some large single mortars further down the coast were also used for dyeing tapa. . . . We must not get the idea, however, that a mortar was only used for one purpose. As it grew in size by use it would undoubtedly serve the purpose for which its size adapted it. . . . The tanning tanks above ordinary high tide are still in operation."

In the Honaunau area some of the artificial concavities also held sticks which marked taboo areas or held wooden religious images. Their steep sides and depth held the sticks or images upright, and both were perhaps also lodged in upright positions by stones. Some of the image holes are now under water (Stokes, 1957:212).

At Pu'u Ehu, the northern end of the ancient route to the refuge shown in Figure 2, there are more than 40 man-made concavities, all under water except at low tide. Some of them are pictured in Figure 5. At Ilio Point (Fig. 2) there are more than 14 similar holes, also usually under water. On an underwater lava shelf west of Ilio Point, a shelf covered with marine growth and which does not show in Figure 2, an additional 29 were located during an extremely low tide in June, 1964.

The Park's famous "egg-crate" *papamu*, on which the ancient Hawaiian checker-like game of *konani* was played, can be shown to visitors only at low tide. Figure 6 emphasizes the resemblance to a modern egg crate. In perfection of manufacture this particular *papamu* has few equals, and it must have been a favored gambling device of resident and visiting royalty.

According to tradition, people who used the ancient route to the refuge from the north (Fig. 2) did not get wet much above their waists, but anyone following that route today would be in water up to his neck. Dry ground was reached at the end of the water route at a lava flat named Akahipapa. In ancient times this slightly convex area, Akahipapa, was a peninsula, with water making it an island only at high tide. Today it

is always an island, and during unusually high tides it is completely submerged. A human-form petroglyph on Akahipapa is frequently covered with water.

During the extremely low tides of the early daylight hours during June, 1964, an unnamed shelf in Kapu-wai cove was uncovered. Local outrigger and skiff operators had long been aware of the shelf, because it is a hazard to navigation of small craft between the cove and offshore fishing grounds. Passageway for boats lies between the northern point of the shelf and Pu'u Ehu. The Park staff took the opportunity to examine the exposed shelf in detail and map its outline and features (Fig. 7). Thirteen major, and six smaller, man-made concavities were found, all covered with marine growth. Figure 8



FIG. 6. "Egg crate" *papamu* at Paieki, just south of the refuge, at low tide, November, 1963. (City of Refuge negative 1012.)

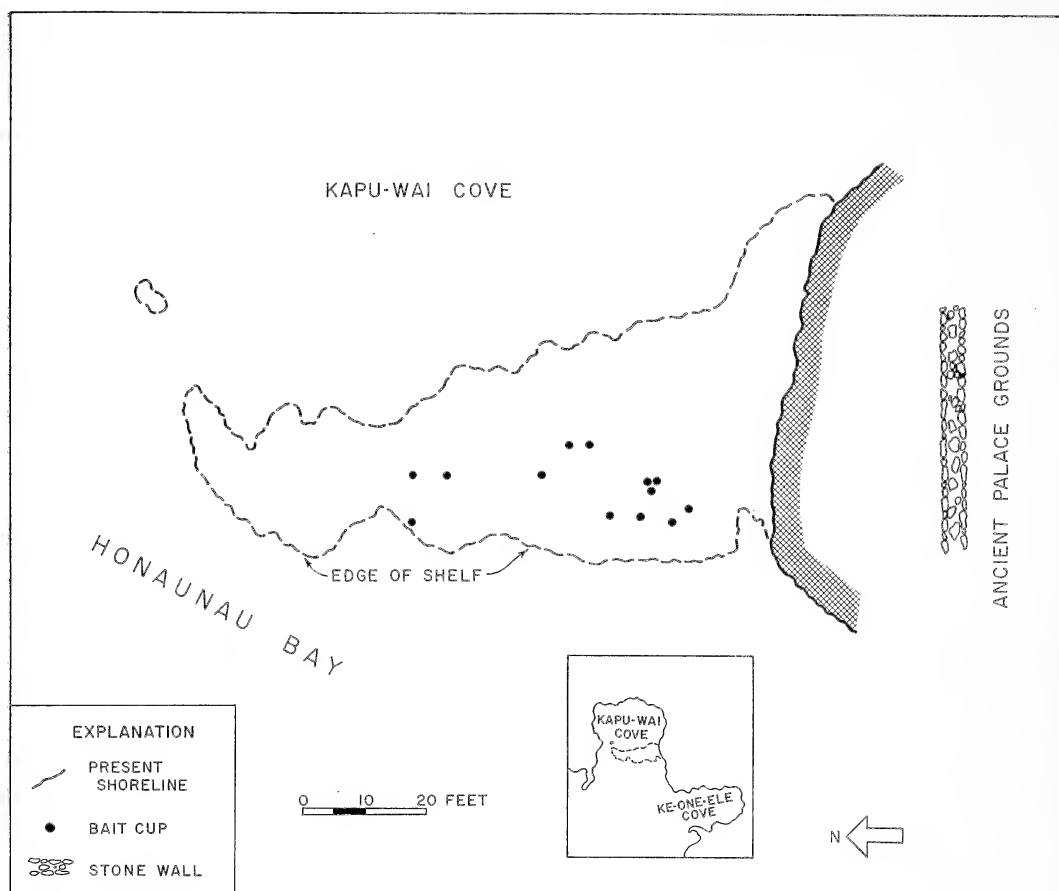


FIG. 7. Map of normally submerged marine shelf projecting from south shore of Kapu-wai cove, Honau-nau Bay. (Map made by Gilbert M. Tanaka, National Park Service, U. S. Dept. of the Interior, at 8 AM, June 8, 1964.)

shows the usual present-day appearance of the shelf area, with a wave breaking over its western edge. Figure 9 shows how the exposed shelf appeared at 8 AM on June 8, 1964.

It is significant that the shelf is unnamed. In 1919, Stokes collected place names for almost all of the minor coastal features in the area, and apparently the large shelf was not mentioned. It had been "lost" for so long that apparently its name and former uses had been forgotten by 1919.

It does not seem logical to assume that the ancient Hawaiians labored with hammer stones and pounders to abrade the artificial concavities, especially the *papamu*, for use only at low tide. Bait cups and tanning tubs would be useless if

they were submerged. There seems to be little question that this tremendous labor went to make features on land which was normally dry, and that since the time when these features were made the land has sunk or the water level has risen.

Without a firm reference point in position and time, it is difficult to estimate the amount of rise of mean sea level relative to the land during contemporary times. Unfortunately, no surveyor set precise benchmarks in 1764. However, we estimate that the relative rise of mean sea level during the last 200 years has been approximately 2 ft. This change helps to explain why the numerous artificial concavities are now usually under water, as well as explaining the

inland creep of the head of Ke-one-ele cove and the wave damage to the 1868 horse ramp. A continuation of the rise will endanger other features. The head of Ke-one-ele cove may move so far inland that bridging may be required to permit access to the restored Hale-o-Keawe temple, if indeed the latter is able to survive in its exposed position. In short, it may prove difficult within the next century or two to maintain the landscape and ancient Hawaiian features as restored in place, to their likely appearance in the 1700's.

GEOLOGICAL ASPECTS

Depression of the shoreline of the island of Hawaii relative to sea level has not been limited to the Honaunau area. Various evidences of depression have been recognized in other areas,

but most of them are vague as to the amount of sinking indicated and the rate at which it is taking place.

Some sinking has been abrupt, during episodes of faulting. During historic time there have been two instances of abrupt localized sinking. During the great earthquake swarm of April, 1868 the area around Kalapana, on the southeast shore of the island (Fig. 1), sank 4–6 ft (Coan, 1869). In 1924, during a swarm of earthquakes on the east rift zone of Kilauea volcano, a graben (fault trough) at Kapoho, at the eastern point of the island, sank 8–12 ft, causing the drowning of coconut trees at its shoreward end (Finch, 1925). The stumps of these trees still protruded from the water in 1940.



FIG. 8. Location of unnamed marine shelf shown in Figure 9, at high tide, June 8, 1964, looking north. (City of Refuge negative 1004.)

The subsidence at Kapoho in 1924 was limited to the fault trough, a zone about 0.4 mile wide. Kalapana also lies in a graben, between two faults, and it appears probable that the sinking in 1868 was restricted largely, if not wholly, to the graben. However, other areas, not within grabens, also have sunk. Just south of Cape Kumukahi, the eastern point of the island, previous to 1960 Hawaiian fishpond walls could be seen submerged 4–6 ft deep in the ocean. (They were buried in part by the lava flow of 1960.) Judging from similar walls elsewhere, they give evidence of a sinking of at least 5 ft. The area is directly on the active east rift zone of Kilauea volcano, and it might be supposed that the sinking was localized, due to a change in volume within the eruptive core of the rift zone, a change similar to that which produces the swell-

ing and shrinking of the rift zone before and after eruptions (Macdonald and Eaton, 1964: 101). However, evidence of sinking exists also at Keaau, 14.2 miles northwest of Cape Kumukahi (Fig. 7). There, according to Eldon S. English and other members of the Shipman family, long-time owners of the property, coconut stumps are submerged below sea level and are invisible even at the lowest tides. The bases of the stumps are buried in sand, and it is difficult to determine just how deep the former ground level now lies below sea level; and also, of course, its original height above sea level is not known. Therefore, the extent of sinking is uncertain, but it must amount to several feet. The recency of sinking also is uncertain, but it appears unlikely that the coconut stumps could have survived more than a few centuries. The



FIG. 9. Unnamed marine shelf projecting northward from the shore of Kapu-wai cove, Honaunau Bay, at low tide, June 8, 1964. Paper rolls mark some of the concavities made by ancient Hawaiians. (City of Refuge negative 1006.)

area is far from the rift zones of either Kilauea or Mauna Loa, and both it and the Honaunau area appear to be examples of a general sinking of the island.

Thus, there is evidence of considerable recent change in the relation of land and sea along the shore of the island of Hawaii, or at least of the southern part of the island occupied by the active volcanoes. A change of this sort could conceivably be the result of either a rise of sea level or an actual sinking of the land mass, or both. A worldwide rise of sea level has indeed been taking place, but during the last century it has amounted to only about 4.5 inches (Gutenberg, 1941:729), and the average rise over the last 2,000 years has been only about 3 inches per century (Shepard, 1964). Thus the changes of roughly a foot per century at Honaunau and of several feet in the last few centuries at Keaau are three or more times as great as the rise of sea level. Most of the change must be attributed to sinking of the island.

The mechanism to explain the sinking of the island is readily available. The great pile of volcanic rocks that forms the Hawaiian ridge is a load on the earth's crust which, if the generally accepted principle of isostasy is correct, should produce a sinking of the crust and the island ridge to restore equilibrium. Seismic evidence suggests that the base of the crust is bowed down beneath the islands (Eaton and Murata, 1960), presumably due to this cause, and the broad trough on the sea floor adjacent to the islands has been attributed to a regional sinking of the crust to partly re-establish isostatic equilibrium (Vening Meinesz, 1940). The older, more northern islands are believed to be partly compensated isostatically (Woollard, 1951), but the island of Hawaii appears to be largely uncompensated (Goranson, 1928; Duerksen, 1943). Although the continuation of the sea floor trough around the island of Hawaii suggests that some sinking, and consequently some compensation, has in fact taken place, the still-growing volcanic mountains must constitute a crustal mass that is tending to sink. The actual sinking indicated by the shoreline evidence almost surely is the result of isostatic adjustment.

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NOTE

Destruction of Marine Flora and Fauna in Fiji Caused by the Hurricane of February 1965¹

M. J. COOPER²

EARLY IN FEBRUARY 1965 a hurricane passed close to the main islands of Fiji. This hurricane brought not only widespread flooding on Viti Levu, the largest island in the group, but also caused unexpected and severe damage to the coral reefs in the southern part of Mbau Water, on the east coast of Viti Levu.

Mr. P. R. Rakoroi, the Officer in Charge at the New Zealand Meteorological Service at Lauthala Bay, gave me the meteorological details and plotted the storm centre on the accompanying map (Fig. 1). The storm began as a small tropical depression to the west of Wallis Island and developed into a severe hurricane as it travelled southwest towards Fiji. The map shows the storm centre on February 7 to be almost stationary, but it was actually moving in a small clockwise circle over northwest Bligh Water before continuing its southwest movement. By February 8 the hurricane was travelling south-southwest, but much more slowly than is usual with these tropical storms. However, by February 9 it had at last picked up speed and begun to move southwest away from Viti Levu. Because the hurricane moved so slowly on the 7th and 8th, torrential rain which always accompanies these tropical storms fell on the island of Viti Levu for a far longer time than is normal. The rainfall figures for Koro-o,

the meteorological station high up on the Rewa watershed in north Viti Levu, and for the meteorological station at Laucala Bay on the coast in southeast Viti Levu, are as follows:

	KORO-O	LAUCALA BAY
	<i>inches</i>	<i>inches</i>
Feb. 6	1.56
7	11.87	1.78
8	31.09	8.25
9	6.79	3.56
10	0.36	0.14

Mr. J. R. Deverell, District Officer, Nausori, gave me details of the flooding caused by this heavy rain. The ground in the hills of the Rewa watershed was completely waterlogged by the 11 inches of rain which fell on February 7, so that the enormous quantity of water from the 31 inches which fell the next day simply poured straight off the hills into the creeks which are the start of the Rewa river system. As this mass of water flowed down to the Rewa River, the tributaries rose to alarming heights. In some gorges the water was up to 100 feet above normal. The Rewa itself at Nausori, where the river is very wide and there is a large flood plain, was 15 ft above normal at high tide, and the whole of Rewa delta was under water.

The main mouth of the Rewa, the Nukulau Mouth, is on the southwest side of the delta. The continuous flow of fresh-water from this mouth is sufficient to keep open a large passage through the barrier reef. This passage was able to carry off the extra water that came down the river during the storm before it caused any

¹ Contribution No. 231, Hawaii Institute of Marine Biology, University of Hawaii. Manuscript received April 28, 1965.

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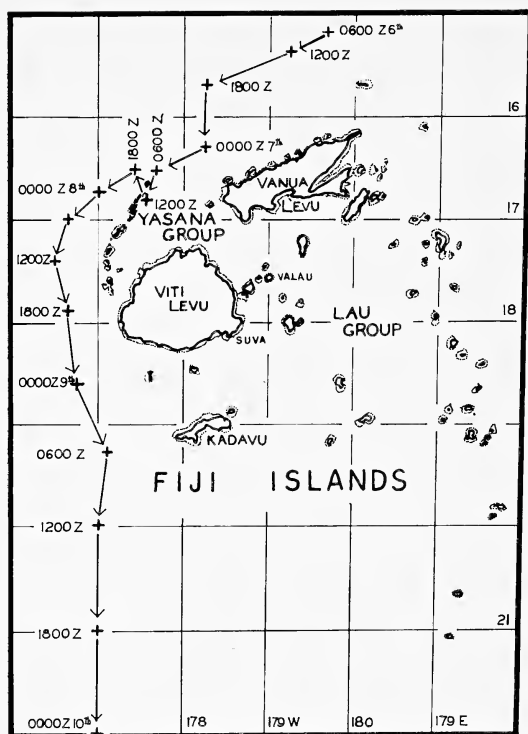


FIG. 1. Track of Hurricane, February 1965.

great damage to the coral reefs in that area. The Navuloa Mouth, one of several minor mouths of the Rewa, is on the north side of the delta. This mouth runs into the south end of Mbau Water, a lagoon-like area bounded to the west by Viti Levu, to the south by the Kamba Peninsula, and the east by a large luxuriant coral reef; to the north it joins Bligh Water, northwest of Ovalau Island 25 miles away. The amount of fresh-water carried by the Navuloa Mouth had not been sufficient to prevent the growth of corals in the area which abounded in fish, mollusks, turtles, and other marine life.

During the February floods the left bank of the Rewa River just below Wainibokasi village gave way, and a mass of floodwater poured into an old bed of the river and was carried northwest across the delta to flow into the sea through the Navuloa Mouth as a great brown, muddy stream. This was seen from Colo-i-Suva, the highest point on the Suva peninsula, by

Sakanasa Rokotuidau and other officers of the Co-operatives Department, who described it as "a brown stain on the sea" which covered the south end of Mbau Water and stretched out into the ocean over the barrier reefs.

For some days after the floods a few dead fish, mostly parrot fish and wrasse, were found on the beaches round Laucala Bay, the Suva peninsula, and Lami. Fishermen reported finding dead fish off the Nasoata and Nasilai mouths of the Rewa, but it is not uncommon for a few dead fish and shells to be found after very heavy rain. However, on February 15 a report came in from Tomberua Island that the sea round the island was covered with thousands of dead fish. I made a trip down the Rewa to Tomberua Island on February 17 to see for myself the extent of the damage, and to talk about it with the people of Kamba village.

Mr. McHugh, owner of Tomberua Island, and the Kamba villagers told me about the dead fish. On February 13 and 14, while they were attempting to salvage a small cutter which had been wrecked on the outer reef during the storm, they passed many dead fish floating on the water. They said that the fish lay in long swathes in the hollows of the waves, 10 ft wide, several fish deep, and stretching as far as they could see. There were fish of all kinds, a few very large fish, most of which had been mauled; many hundreds of medium-sized fish, small barracudas, parrot fish, wrasse, red and grey snappers, groupers, eels, surgeon fish, mullets, puffer fish, and trigger fish; many thousands of very small fish, brilliantly coloured damsel fish and butterfly fish, small eels, and young fish of all kinds. On February 15 and 16 many of these fish were washed up on the beach at Tomberua, where they were buried, but very few were cast up on the beaches of the Kamba peninsula. The Kamba people, who are expert fishermen, told me that they had never heard of anything like this happening before. The floods of 1929, 1931, 1954, and March 1964, although causing heavy damage to property and food crops and mortality amongst livestock, did not affect any reefs to this extent.

I walked on the Tomberua reef at half tide

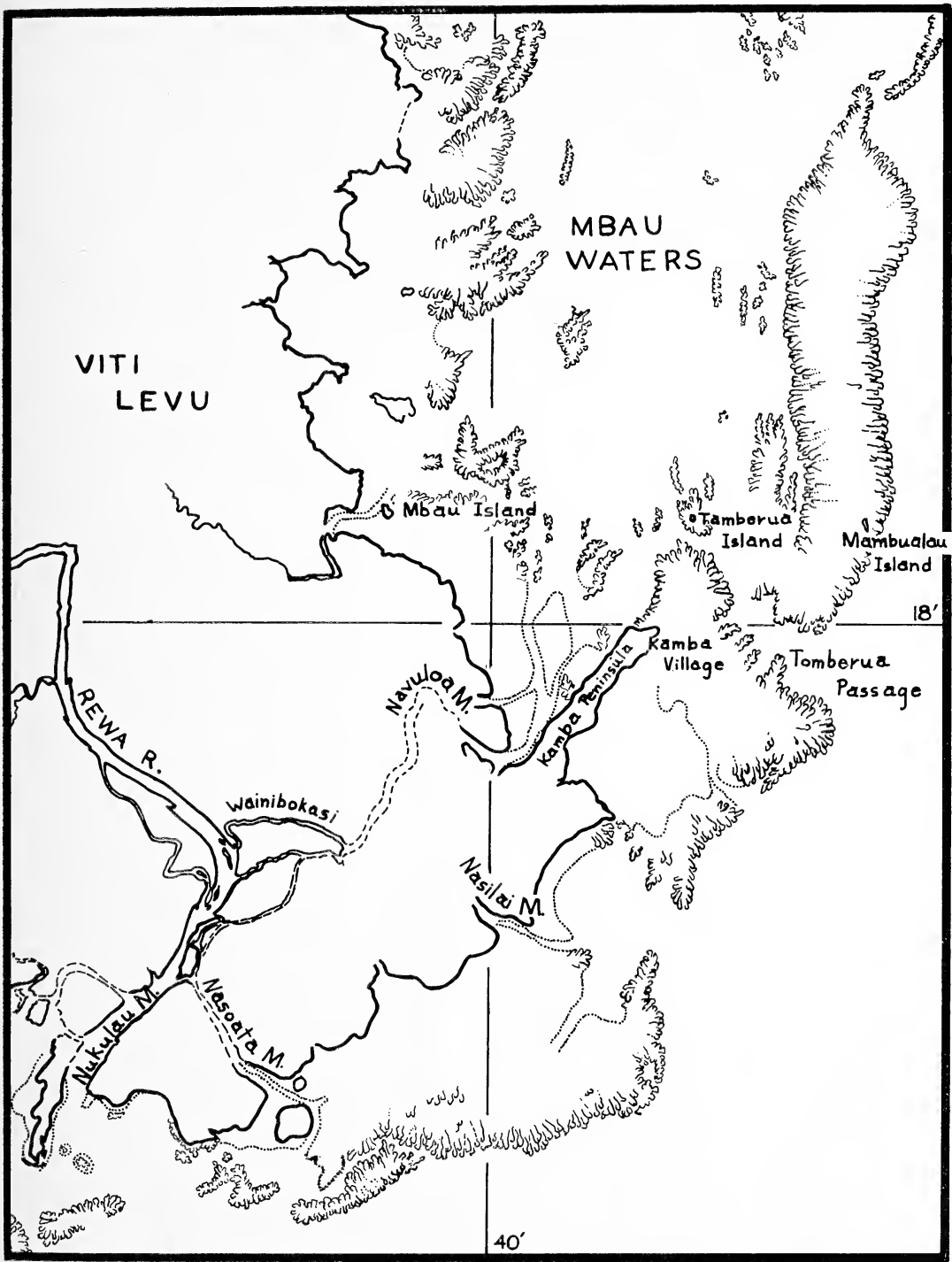


FIG. 2. Map of Mbau Waters, Fiji.

and wandered slowly along the edge of the receding water. I stayed out on the reef until the tide turned and began to cover the reef again. Nearly every living thing, plant or animal, on the reef was dead. The reef itself was a dull brown, the sand a dull grey. In places there were patches of white or black, the putrefying remains of unidentifiable sea creatures. Shells of many kinds were lying on the sand, on what had presumably been a mat of green alga, now a yellowish-grey rotting mass. There were thorny oysters gaping white on the stones, there were cockles, clams, tellins, scallops, augurs, black-mouthed pinnas, pink olives, and the carapaces of sand dollars and heart urchins scattered everywhere, with foul-smelling clumps of rotting *Halimeda*. Farther out among the tide pools were many kinds of cones, miters, cowries, limpets, strombs, spider shells, and chitons, together with the fluorescent whiteness of burst and rotting holothurians. Some of the shells had already been occupied by a species of black and yellow hermit crab, but these crabs were very languid and obviously dying. I turned over a few stones: they were black and slimy underneath, a dying worm or two floated out, and the decaying remains of a brittle star. There were no small sponges, algae, anemones, shell eggs, or any other organisms left alive under the stones or in the sand, which was black and foul under the surface. On the very edge of the reef the smell was really horrible. There were large putrefying masses of soft corals, decaying remains of many unidentifiable creatures lying on the dull, brown, dead corals. I peered into the deeper water. Even the sea seemed to smell of decay, and I could see no sign of any coloured living coral nor the bright green of any alga. All seemed dead.

This dismal picture was relieved a little when I found a very lively, very belligerent red-eyed crab, and, in one or two of the deeper tide pools near the edge of the reef, I found that a few small fish had already moved in, or perhaps had survived the kill. They were very few in number and appeared to be a species of goby, one small *Pleisops*, and three species of *Abudefduf*, possibly *sordidus*, *zonatus*, and *sax-*

atilis. I noticed that these live fish were in pools that had a rock or clear sand bottom, with no rotting algae, and which possibly had a higher oxygen content than other pools. In one shallow pool I found a beautiful green and blue cowfish, *Lactoria* sp., which was grazing on rotting algae and appeared unaffected by the foul conditions. I saw several rather large eels, *Gymnothorax picta*, which were swimming with their heads sticking out of the water and seemed completely fearless. On my way back to the island I found several apparently healthy colonies of a species of *Nerita* and one small bright green tuft of *Enteromorpha* growing in a strong current near the edge of the reef. A frequent splashing sound attracted my attention and, wading out into the sea, I found it was caused by a huge school of sardines, or "dan-iva" (*Clupea* sp.?), frantically feeding on the cloudy brown detritus from the reef.

The Kamba people told me that during the flood the whole sea around Tomberua Island, off the Kamba peninsula, and right out over the reef by Mumbualau Island was muddy, and that when they swam in it they found that it was quite fresh, "like the river." It seems certain that this freshening of the water was responsible for the initial mortality. The Department of Agriculture says that there had been little or no use of pesticides or herbicides prior to the floods which might have been washed off the land into the rivers, nor does there seem to have been any other form of pollution which could have caused the damage. The many fish and other plants and animals killed by the fresh-water began to putrefy, and this in turn caused the death of other organisms by using up the available oxygen and polluting the reef with hydrogen sulphide and other products of decomposition.

It will be very interesting to watch the regeneration and repopulation of these reefs to see if there is any marked or permanent ecological change. In recent years some fish caught in Mbau Water have been known to cause ciguatera poisoning; these are chiefly *Lethrinus miniatus* and *Lutianus bohar*, although other lethrinids may be poisonous as well. Cases of

poisoning from fish caught there were rather infrequent but continual. According to one hypothesis, ciguatera increases when "new surfaces" are exposed to settlement by blue-green algae (Randall, 1958). As yet no cases of fish poisoning have been reported. The Kamba people, who traditionally fish in these waters, are most concerned in case the poisoning should become much worse as a result of the extensive damage and are watching the area with great interest.

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Book Review

J. L. Gressitt et al. *Insects of Campbell Island*. Pacific Insects, Monograph No. 7. Bernice P. Bishop Museum, Honolulu. 1964. 663 pp., approx. 330 figs.

THIS, the seventh, volume of the monograph series on Pacific insects is more than the title suggests, as it is actually an intensive taxonomic study of the entire terrestrial arthropod fauna of Campbell Island. Corollary to the recent greatly increased interest in Antarctica has been a corresponding increase in interest and activity concerning the biota of the subantarctic islands, of which Campbell is a member. Partly through financial and logistic support of various recent antarctic expeditions, rather thorough collections of the terrestrial arthropods of Campbell Island have been made. The nearly completed results of the study of these collections are published in the present volume.

An introductory section on the history, geography, geology, flora, weather, and climate of

the island precedes the detailed taxonomic portion. The body of the volume is the taxonomy of the approximately 300 species of arthropods collected. They represent over 100 families ranging from amphipods to Hymenoptera. As presented they constitute a peculiar and most interesting fauna, of which approximately 50% are endemic forms. Concluding sections are on insects and insect parts found in the accumulated peat, on the ecology of the island, on zoogeography, dispersal, and evolution. As is stated in the introduction, the zoogeographic conclusions are only preliminary and must remain so at least until the faunas of the other subantarctic islands are also satisfactorily known.

A supplement contains odd bits and pieces on the faunas of Auckland and Macquarie islands.

The present work maintains the quality that we have come to expect from the Entomological Department of the Bishop Museum.—L.D.T.

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

ALBERT H. BANNER and DORA M. BANNER

*Alpheid Shrimp of the Pacific Ocean, X. Collections from Fiji,
Tonga, and Samoa*

GEORGE E. CANTWELL

Relationships among Species of Parapercis

B. J. LANDRUM

Bilateral Asymmetry in Meristic Characters of Salmon

JOHN W. WELLS

*Indo-Pacific Scleractinian Corals, Part 4. Stylocoeniella
guentheri*

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*Echinoidea Collected by the Royal Society Expedition to
Southern Chile, 1958-1959*

HAROLD W. HARRY

Land Snails of Ulithi Atoll, Caroline Islands

ANN M. CAMERON

Behaviour of the Soldier Crab, Mictyris longicarpus

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*Skeletal Sodium, Manganese, and Iron in Dendraster
excentricus*

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Vertical Circulation off the Ross Ice Shelf

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*Bleekeria compta: A New Binomial for a Hawaiian
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(Continued on inside back cover)

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part X. Collections from Fiji, Tonga, and Samoa¹

ALBERT H. BANNER and DORA M. BANNER²

THIS IS THE SECOND PAPER in a series on the collections made by the senior author in 1954 while on a Yale University–University of Hawaii–Bishop Museum Grant; it deals with those shrimps collected in the Fiji, Tonga, and Samoa archipelagoes.

The study of these shrimps was supported in part by a series of grants from the National Science Foundation (G-1754, G-3863, G-9937). The collection in 1963 was made in part under National Science Foundation Grant GB-796, and under a special grant from the University of Hawaii.

This paper was prepared in final form in December 1961, complete with plates, maps, locality records, etc., but it was destroyed in the fire at the Hawaii Marine Laboratory (see Banner and Banner, 1962). Lost also in the fire were the specimens in the collection and the field notes. The sections of the paper dealing with Fiji, Tonga, and Western Samoa were salvaged in part from the partially burned original study notes and in part from the first draft of the text; for American Samoa we were able to make another collection which partially replaced the lost collection. Certain ambiguities in the preliminary notes could not be resolved for this final completed paper by reference to the original specimens, as is normally done. More harmful to the completed study were the loss of the plates and the data on collections. It is with many misgivings that we publish this paper, especially the descriptions of new species, without the specimens, plates, and data; however, because the alpheid fauna of the central Pacific is so little known, we felt that this paper would be of use to future workers. It is hoped that

when other workers find specimens agreeing with our new species and subspecies from near the type areas, they will designate them as neotypes and deposit them in a museum or other institution.

During the summer of 1963 we were able to spend about two weeks in collecting again from Tutuila. On this second trip we revisited some of the places where collections were made in 1954 and also collected from localities not reached on the previous trip.

The studies made with this grant attempted to investigate the zoogeographic distribution of the alpheid shrimp in the central Pacific—presuming that with extensive sampling an accurate picture of the shrimp fauna of an archipelago could be obtained. The two series of collections made nine years apart on the small island of Tutuila in American Samoa give an opportunity to assess the reliability of our samplings as indicators of the total alpheid fauna. In 1954 the collections were made at Tutuila along the windward (southern) coast on the narrow fringing reefs and within Pago Pago harbor; then, to complete the picture of the Samoan alpheids, further collections were made along the lee or northern coast of Upolu, on the wide fringing to barrier reef. During the 1963 trip to Tutuila (it was not possible to make additional collections on Upolu) some of the localities sampled in 1954 were again visited. However, no collection could be made at some of the earlier localities because of changes in topography. For example, Tafuna in 1954 was a sandy beach and in 1963 it was an airport. Furthermore, because better transportation was available, additional localities were visited. Therefore, the two collections are not strictly comparable, but they give some indication of how well the fauna was sampled in each case. The collections are summarized in Table 1.

¹ Contribution No. 239, Hawaii Institute of Marine Biology. Manuscript received January 22, 1963.

² Department of Zoology and Entomology, University of Hawaii, Honolulu.

TABLE 1
NUMBERS OF SPECIES AND SPECIMENS COLLECTED IN SAMOA

COLLECTIONS	UPOLU	TUTUILA	TUTUILA
	1954	1954	1963
Species and subspecies	32	38	34
Specimens	705 (approx.)	715 (approx.)	523
Species and subspecies not found on Tutuila (both years)	4		
Specimens in these species and subspecies	13		
Percent* of total specimens	0.67		
Species and subspecies not collected from Tutuila, 1963		17	
Specimens in these species and subspecies		63	
Percent of total specimens		3.2	
Species and subspecies not collected from Tutuila, 1954			13
Specimens in these species and subspecies			117
Percent of total specimens			6.0

* Percentages are based on a total of about 1,950 specimens.

Two conclusions may be drawn from Table 1. First, a single series of collections, such as that made at Tutuila, or on both Samoan islands (or in Fiji and Tonga, or most of the other archipelagoes that have been or will be reported upon), does not approach a complete account of the shallow water fauna, even if different types of environment are deliberately sought. Thus, it is estimated that the combined Samoan collections, listing 58 species and subspecies, lack somewhere between 25 and 50% of the species found in the archipelago. Second, if the number of species is far from the total number that could be recorded, those specimens not collected are relatively rare in the environments that could be sampled. For example, of the 47 species collected on both trips to Tutuila, 17 or almost 33% were collected on the first trip but not on the second, yet these 17 species were represented by only 83 specimens of the 1240 collected, or 6.9% of the total for the island.

COLLECTION LOCALITIES

All copies of detailed field records of the collecting localities were destroyed in the fire, but fortunately maps showing geographical location of the field stations were in the hands of the staff artist. These field locations were sufficient to recall to the senior author some details of the collecting sites. Dates were obtained from personal letters.

Stations in Fiji, Viti Levu

BF 1-18. At Korolevu, on the southern coast, during the week 14-20 March 1954. Here the reef investigated was of fringing type lying along the shore, well within the barrier reef complex of the archipelago. The beach was of beach rock and sand; the immediately adjacent water was the "lagoon," perhaps 2 or 3 ft deep at low tide. Seaward the reef platform rose to be exposed at low tides, but with the numerous potholes and cracks bearing living coral; the

outermost edge of the reef was of coral and coralline algae. A few hundred yards away from the collecting area was the mouth of a small stream; the coral reef did not extend across its mouth, but dropped off abruptly to a sandy bottom about 20 or more ft deep. The stations were on a line crossing the reef from the innermost lagoon to the seaward edge (no diving was done off the seaward edge because of storm waves) and at the edges of the stream basin; the exact location of the individual stations cannot be recalled.

BF 19–20. On the barrier reef protecting Suva Harbor, 11–13 April 1954. Here the barrier reef surface was largely exposed at low tide but, except for the seaward edge, was almost devoid of living coral, being composed instead of broken coral fragments. The first station was on the seaward sector of the reef, the second on the lagoon side.

Stations in Tonga

All collections were made on Tongatabu between 27 March and 7 April 1954.

BT 1, 2, 4, and 6. On the sandy shore and bottom of the harbor of Nuku'alofa (near the point marked on U. S. Army Map Service Map [x622, 1943 ed.] as "Mine Layers' Pier") and the specimens were collected from dead coral heads between the intertidal zone and water about 8 ft deep.

BT 3 and 14. Off Nukunuku Island near the mouth of the large brackish lagoon; most specimens were collected under dead coral boulders lying on the broad sand and dead coral flats, and were exposed at low tide.

BT 7 and 8. On the Nuku'alofa side of Pangaimotu in relatively protected waters, BT 7 being from living and dead coral slightly below the intertidal zone, BT 8 being somewhat deeper. A moderate amount of growing coral was found in this area.



FIG. 1. Map of the area of the South Pacific covered by these collections.

BT 9. On the channel (northern side) of Pangaimotu, where the currents were strong and living coral was flourishing; most specimens came from coral heads that could be collected by diving 6–10 ft.

BT 10 and 11. On the south coast of Tongatabu, south of Tokomololo village. Here the island coast was bold, in places with sharp cliffs. The shore margin when under the influence of southern storms may have extreme surf. The reef was marked by a narrow, shallow "lagoon," knee- to waist-deep, inshore from the marginal living coral and coralline ridge; the seaward edge of the ridge was serrate with surge channels, and the bottom drops off almost immediately into deep blue water. The collections were made from encrusting coral and coralline algae from the "lagoon"; no collections could be made from the ridge because of heavy surf.

BT 12 and 13. In the district of Kologna on the fringing reef in water up to several feet below the low tide zone. Here waves sweeping across the outer reef promoted the growth of coral, and coral sand occurred only in pockets.

BT 15. In the lagoon, Fanga Uta, near Havelu village. The lagoon was shallow, brackish, in large part with a mud bottom, and surrounded by halophilic plants such as mangroves. Some of the specimens were collected from the mud substrate, and some were from old and decaying heads of dead coral.

BT 16. The inner margin of a seaward reef protecting the harbor of Nuku'alofa near Lahi passage in a region of vigorous coral growth;

specimens came from coral heads from the intertidal zone down to about 20 ft deep.

BT 17. An area south of the village, Houma, along the cliffed shore, similar ecologically to BT 10 and 11; these specimens also came from coral heads in the "lagoon" behind the coralline ridge.

Stations in American Samoa, Tutuila

Collections were made from 18 to 24 April 1954.

BAS 1, 2, 3, and 4. The Utelei section of Pago Pago harbor, made on a transect from low tide zone (station BAS 1) across the narrow reef to water about 10 ft deep (station BAS 4).

BAS 6, 7, and 8. On a similar transect in the Fagaalu section of Pago Pago Harbor. BAS 6, the innermost station, was made at low tide zone, BAS 7 in a dredged depression about 8 ft deep, and BAS 8 on the outer portion of the fringing reef.

BAS 9. On the opposite shore of Pago Pago harbor, on a vigorously growing reef. Specimens were collected from coral by diving in 6–20 ft of water.

BAS 5, 13, and 14. At "Lion's Head" (the Samoan name is not available). Here the fringing reef was narrow and wave-swept; the collecting was done in the protection of a rock set on the reef (30 or more ft high, and possibly 100 or more ft wide at the base), in water about 2–4 ft deep at low tide, with moderate to strong surge. Specimens were collected from encrusting and massive corals.

BAS 10, 11, and 12. Off Tafuna (a collecting area now largely destroyed by the new airport). BAS 10 and 11 were in shallow water which evidently could become brackish at times of heavy rainfall. The bottom was largely sand. BAS 12 was farther from shore but still in wading depth of water.

Stations in American Samoa, Tutuila

Collections were made from 14 August to 1 September 1963. (References are to U. S. Coast and Geodetic Survey Chart #4190, 1962 ed.).

BP 1. The same as BAS 5, 13, 14.

BP 3. On Tower Rock Reef (sometimes called Flower Pot Rock) at the western side of the entrance to Pago Pago bay in about 2–3 ft

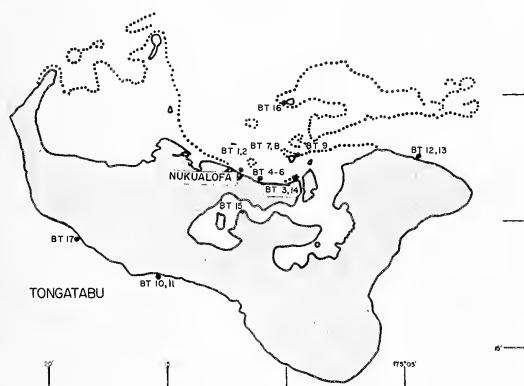


FIG. 2. Map of Tongatabu showing collecting stations.

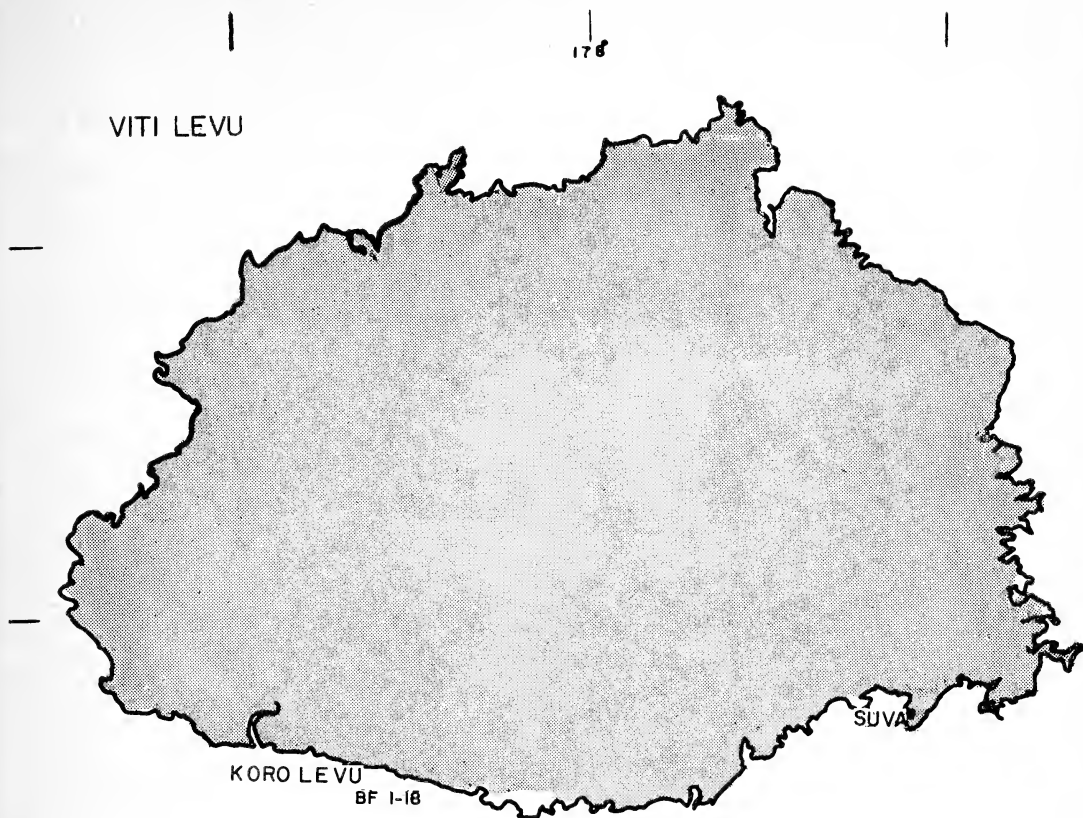


FIG. 3. Map of Viti Levu showing collecting stations.

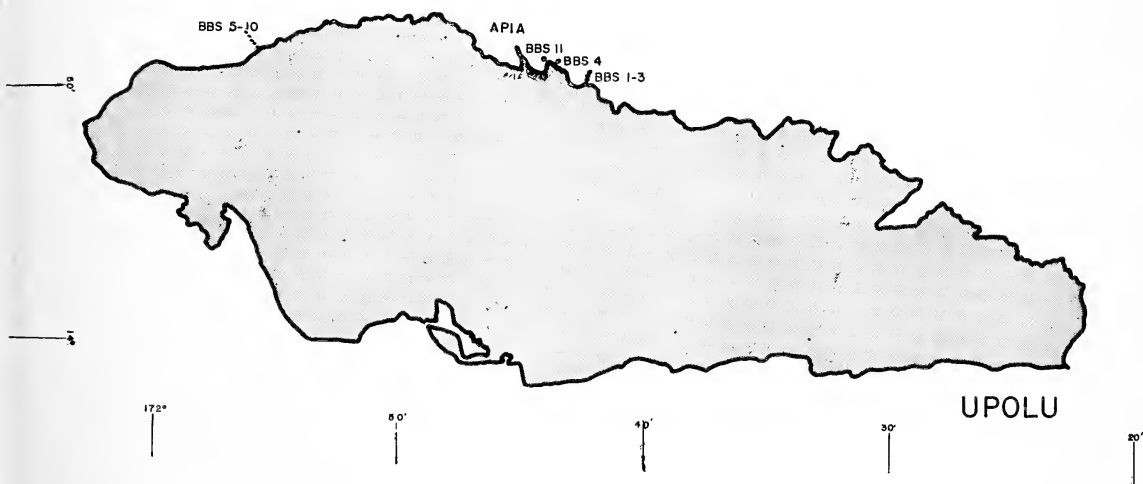


FIG. 4. Map of Upolu showing collecting stations.

of water. Specimens were collected from dead and live coral which was found in depressions at the inner edge of the reef which is several hundred yards wide.

BP 4. At Alofau on Fagaitua Bay on the outer face of the fringing reef in water approximately 3–10 ft deep. Specimens were collected from living and overgrown heads of dead coral.

BP 5. At Utumea on the southeastern side of the island, from the middle reef flat, at about 0 ft tide level. Collections were made from old, rather solid, heads of dead coral.

BP 6, 6a, 7, 8, and 9. Various localities on the reef flat at A'umi (east of Lau'i'i). BP 6 was the inner area of the reef; BP 6a was located in an encrusting tube; BP 7 was from corals taken in a protected portion of reef flat; BP 8 and 9 were located in the surge zone.

BP 10. At Leone on the southwestern side of the island. Specimens were collected from heads of dead coral from the reef flat in water 2–3 ft deep. The water was brackish and carried silt from the land; the bottom was fine sand and mud mixed with a great deal of organic detritus.

BP 11. At Pago Pago between Aua and Breaker Point. Specimens were collected from heads of coral lying near the surf zone.

BP 12, 12a, 13. At Lau'i'i, in water 2–3 ft deep; BP 12 was near the middle reef; the specimen from BP 12a was found commensal with a brittle star; and BP 13 was near the reef edge.

BP 14 and 15. In the entrance to the lagoon near the airport (Cocoanut Point on the chart). The area was subject to more than the usual amount of fresh water run off. BP 14 was taken from dead coral heads in about 3 ft of water from a shallow broad flat where the bottom was of silty sand with organic debris. BP 15 was located under boulders on the shore at about middle tide zone, in very fine sand.

BP 16. At Fangasa'a, located on a deep inlet on the leeward side of the island. Specimens were collected from dead coral heads on the outer face of a flourishing reef on the west side of the bay in about 3–15 ft of water.

Stations in Western Samoa, Upolu

Collections were made from 25 April to 12 May 1954.

BBS 1–3. On a transect across a broad fringing reef at Fagalii east of Apia. BBS 1 was the

most inshore; BBS 3 was almost at the surf zone.

BBS 4. An inshore area at Vaiala a short distance east of Apia.

BBS 5–10. On a transect across the broad fringing reef at Vailutai in the Fasito'outa district; here the reef was several miles broad, but without a boat lagoon as is found closer to Apia. The maximum depth on the reef was approximately 8 or 10 ft, rising again to a shoal reef front; the submerged reef flat was sandy with scattered coral; the reef front consisted of vigorously growing coral. The stations ranged from the shore, where there were freshwater springs below the low tide zone, to the outer face of the reef front. The stations were not in numerical order.

BBS 11. On a vigorously growing coral reef, in depths to about 20 ft, on the eastern side of Apia Harbor near Matautu.

AUTOMATE de Man

Automate gardineri Coutière

Automate gardineri Coutière, 1902. Mus.

Hist. Nat., Bull. 8(5):337; 1903. Soc.

Philomath. Paris, Bull. 5(2):1–4, figs. 1–8.

Automate johnsoni Chace, 1955. U. S. Nat.

Mus., Proc. 105(3349):13, fig. 7.

LOCALITIES: Tonga: 1 specimen from BT 8. Samoa: 1 specimen from BAS 1; 1 from BAS 11; 1 from BP 5.

DISCUSSION: In addition to these specimens, and those previously reported from Saipan and under the name *A. johnsoni* (Banner 1956: 321), there are some in the collections from the Cook, Society, and Marshall islands to be reported upon in later papers, a total of 17 specimens. Unfortunately many of these specimens are small and broken, and most are lacking their chelae.

This series of specimens appears to bridge all but one of the criteria used by Chace to separate *A. johnsoni* from *A. gardineri*. He stated that the rostrum in the form found in the Marshall Islands was triangular instead of rounded; in this series both types of rostrums occur, and in one large specimen from Eniwetok the rostrum is rounded. In *A. johnsoni* the second antennular article is 2.5 times as long as broad, while in *A. gardineri* the same article is 4 times as

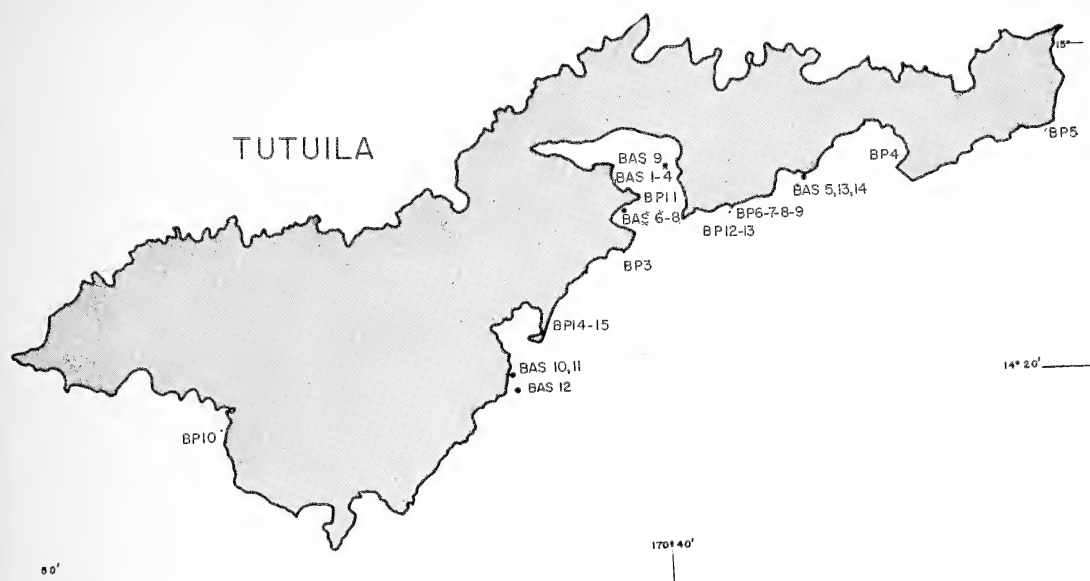


FIG. 5. Map of Tutuila showing collecting stations.

long in the male, 3.5 times as long in the female; in these specimens it varies from about 2 times to more than 3.5 times as long as broad. The stylocerite is supposed to reach slightly beyond the distal margin of the proximal segment in *A. johnsoni*. In the Saipan specimens none reached to the end. In the others two did not reach to the end; four reached to the end; and five reached beyond the end of this article. The antennal scale in *A. johnsoni*, instead of extending to the middle of the second antennular article, is supposed to reach to the distal fifth; in these specimens both conditions are found, as well as intergrading steps between. In the Saipan study a difference was noted in the length of the carpal articles of the second legs, with the second article 1.8 in *A. gardineri*, 1.2 in *A. johnsoni*, and 1.3 times the length of the first article in the Saipan specimens; in these newer specimens the ratio has been found to vary from 1.2 to 1.5, but most specimens were lacking their second legs. The only remaining difference remarked by Chace is the occurrence

of slight grooves in the carapace on either side of the rostrum which are present in *A. gardineri* alone. These grooves were not seen on any of these specimens, but because of the thin, transparent nature of the exoskeleton in this region of the body it is very difficult even to see the rostrum. Moreover, since the exoskeleton is rather soft, these folds may actually be artifacts. In any case they do not appear to be a valid criterion for the separation of the two species.

Unfortunately, there are not enough specimens from any one locality, and those we have are not complete enough to permit evaluation of their differences from other species of this genus described from the Indo-Pacific. "*A. species*" of de Man probably is this species; moreover, this species is possibly a synonym of *A. dolichognatha* de Man, for the principal difference between the two species is the form of the large chelae of the male and female, a difference that may be the result of maturity. *A. anacanthopus* de Man and *A. salomoni* Coutière appear to be distinct species.

ATHANAS Leach³*Athanas djiboutensis* Coutière

For full citation see Banner and Banner (1960:140).

LOCALITIES: Samoa: 1 specimen from BP 5; 2, BP 7; 2, BP 8; 2, BP 10; 3, BP 11; 4, BP 13. Specimens were also taken from Western Samoa, Tonga, and Fiji.

Athanas parvus de Man

For full citation see Banner and Banner (1960:141).

LOCALITIES: Tonga: 7 specimens. Samoa: 4 specimens.

Athanas rhothionastes Banner and Banner

Athanas rhothionastes Banner and Banner, 1960. Pacific Sci. 14(2):142-146, fig. 2.

LOCALITIES: Samoa, Tonga, and Fiji.

Athanas areteformis Coutière

For full citation see Banner and Banner (1960:138).

LOCALITY: Samoa: 1 specimen from BP 11.

Athanas indicus (Coutière)

For full citation see Banner and Banner (1960:149).

LOCALITY: Samoa: 1 specimen from BP 11.

Athanas borradailei (Coutière)

Fig. 6

Arete borradailei Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):861, fig. 133.

LOCALITY: Samoa: 1 specimen from BP 8.

DISCUSSION: Our specimen agrees with Coutière's with the exception of the rostrum. The rostrum reaches only to the first quarter of the visible part of the first antennular article instead of to the end of the second. We believe that this

³ The sheets recording the collection data for the members of this genus were destroyed in the fire of the Hawaii Marine Laboratory, and the records cited below (with the exception of those for the five species in the new collections from Tutuila) are taken from Banner and Banner (1960:138-154).

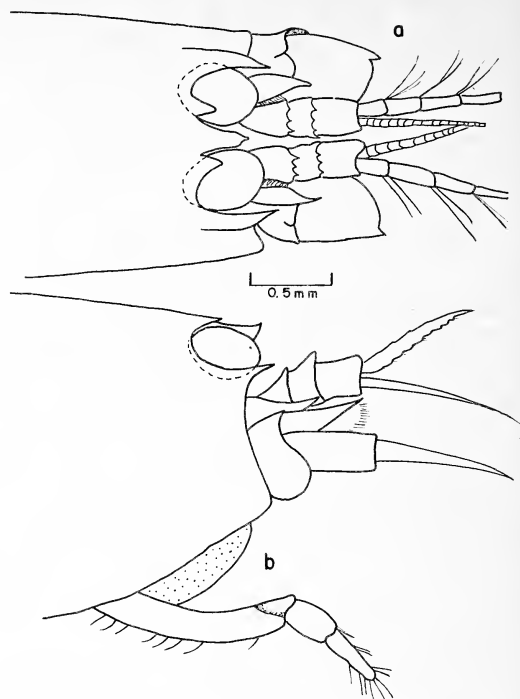


FIG. 6. *Athanas borradailei* Coutière. 7 mm female from station BP 8. a, b, Anterior body region.

is a growth anomaly and, unless other specimens are collected which show this difference, we assume that our specimen belongs to Coutière's species.

Athanas dorsalis (Stimpson)

For full citation see Banner and Banner (1960:151).

LOCALITY: Fiji: 1 specimen.

Athanas polynesia sp. nov.

Fig. 7

TYPE: A 7-mm male collected at Alofa (BP 4) on the island of Tutuila from a head of dead coral collected in the outer reef area in water about 3-10 ft deep. Two other males were collected at the same locality.

DESCRIPTION: Rostrum reaching to end of second antennular article with distal portion of dorsal margin gradually curved upward, but with all of inferior margin curving upward toward tip; inferior margin bearing small tuft of setae in small, sharp notch about halfway from

eyes to tip. Supracorneal teeth short, triangular, reaching about two-thirds the visible length of cornea; extracorneal teeth longer, reaching beyond cornea, almost to end of first antennular article.

Antennular peduncle short, with visible part of first antennular article the longest, second and third articles subequal. Superior distal margins of first and second antennular articles bearing 4 teeth. Stylocerite heavy and acute with tip reaching end of second antennular article. Scaphocerite with outer margin straight and with broad squame reaching slightly beyond end of antennular peduncle; lateral spine only slightly longer than squame. Carpocerite thick and as long as antennular peduncle. Basicerite broadened, without spine.

Mouthparts protrudent, with inflated labrum; incisor lobe of psalidome of mandible also expanded, dish-shaped with fine teeth and molar portion reduced.

Chelae similar in form, but with large chela 1.3 times the length of the small chela. Large chela about 1.5 times as long as broad, with fingers occupying the distal third. Inner face convex, outer face only slightly convex, distal portion of superior margin flattened, leaflike, and bearing strong, forward-directed papillae from middle of chela to dactylar articulation, each papilla bearing one heavy seta. Outer and inner face without papillae. Lower margin opposite dactylar articulation flattened, leaflike, and bearing six setiferous papillae similar to those of upper margin. Outer and inner faces smooth. Dactylus heavy, curved, with tip crossing at fixed finger; without papillae but with fine setae. Ischium heavy, about half as long as merus, bearing six to eight movable spines on both the inferior and superior margin, with three final spines on either margin on distal shoulder. Merus unarmed, 1.7 times as long as broad at its widest point, flattened where it joins the ischium but inflated, almost cylindrical in section, at about two-thirds of its length and most narrow where it joins the carpus. Carpus 1.3 times as long as merus, proximally very thin and narrow, and curved to admit flexure, distally greatly expanded. Inner side excavate with leaf-like projections to encompass basal portion of palm where joint is flexed. Small cheliped of

similar configuration but with fewer setae, ischium with fewer spines.

Merus of second leg 1.3 times longer than ischium. Carpus of four articles with ratio of 10:6:3:7.

Third leg robust. Ischium unarmed, 0.5 length of merus. Merus inermous, 2.5 times as long as broad; carpus 0.5 as long as merus, armed with single strong movable spine on distal end of inferior margin. Propodus 1.3 times as long as merus. Inferior margin bearing four pairs of movable spines, and two strong spines on the inferior side of the dactylar articulation. Dactylus simple, curved, 0.4 as long as merus.

Telson slender, 3.5 times as long as broad at its posterior margin. Anterior margin twice as wide as posterior margin. Posterior margin extended and rounded.

DISCUSSION: In the key published in the revision of the genus *Athanas* (Banner and Banner, 1960:138) this species shows a relationship to *Athanas verrucosus* Banner and Banner, *Athanas borradailei* (Coutière), and *Athanas ghardaquensis* (Ramadan). It may be separated from *A. verrucosus* by a series of characteristics, probably the most reliable being the four articles of the carpus of the second leg, and the lack of papillae on the face of the palm of the chelae. A difference is also found in the greater breadth of the large chela of *A. verrucosus*, which is 2.2 times as long as broad, while in *A. polynesia* it is 1.5 times as long. This species is similar in frontal region and carpus of the second leg to *A. borradailei* (Coutière) (1905: 861) but the chelae of *A. borradailei* are more slender and without papillae, and the ischia and meri of the chelipeds are without spines. *A. ghardaquensis* (Ramadan) (1936:15) may be separated from this species by its lack of marginal papillae on the chelae, and by the fact that in *A. ghardaquensis* the chelae are symmetrical.

SALMONEUS Holthuis

Salmoneus tricristata Banner

Salmoneus tricristata Banner, 1959. Pacific Sci. 13(2):131, fig. 1.

LOCALITY: Samoa: 2 specimens from BAS 10.

DISCUSSION: The larger female of these two

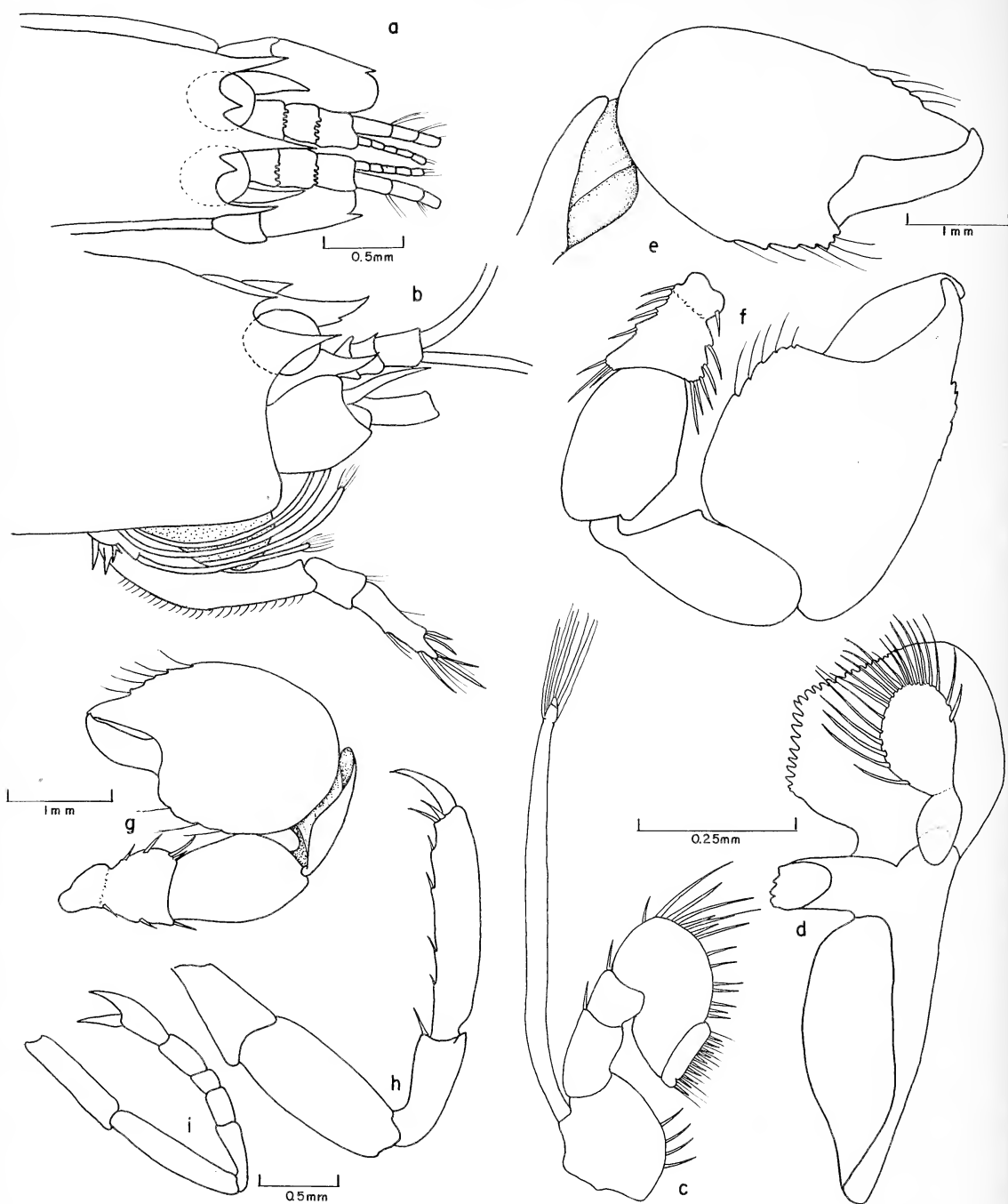


FIG. 7. *Athanas polynesia* sp. nov. Type. 7 mm male from station BP 4. *a*, *b*, Anterior body region; *c*, second maxilliped; *d*, mandible; *e*, large cheliped inner face; *f*, large cheliped outer face; *g*, small cheliped inner face; *h*, third leg; *i*, second leg.

specimens has both chelae intact; they appear to be identical with those of *S. sibogae* (de Man). The chelae will be described in a later paper of this series.

Salmaneus sibogae (de Man)

For full citation see Banner and Banner (1964:86).

LOCALITIES: Fiji: 2 specimens from BF 2; 2, BF 4; 1, BF 5; 1, BF 12; 1, BF 18; 2, BF 19; 2, BF 20.

DISCUSSION: These specimens and some from other localities, especially Eniwetok, were examined closely to determine the extent of variation in certain of the taxonomically important characteristics. The telson is quite uniform, and in all normal specimens the notch is trapeziform; in those few specimens where the notch is not of this shape, the telson is definitely malformed, with poorly developed posterolateral lobes and lacking in some cases the terminal spines on the malformed side. The rostrum, however, is quite variable. The tip may reach from the end of the second antennular article to the end of the third. The breadth usually is equal to the length (the triangle measured with the baseline at the most posterior portion of the notch between the rostrum and the orbital teeth), and its sides are concave; but in some specimens the length is up to 1.5 times the breadth of the base. The orbital teeth are somewhat variable, but never reach to the end of the first antennular article. The stylocerite, scaphocerite, and carpocerite are surprisingly uniform, with the stylocerite reaching to the middle of the third antennular article, the scaphocerite reaching to or slightly beyond the end of the third antennular article, and the carpocerite reaching only to the middle of the second antennular article. Inasmuch as the stylocerite remains rather constant and the rostrum variable, in some specimens the stylocerite is longer, and in others shorter, than the rostrum. No variation was noted in the thoracic legs, although they were not studied closely. There is no marked sexual dimorphism in the form and size of the large or the small chela.

This species is closely related to *S. latirostris* (Coutière), *S. hilarula* (de Man), and *S. mau-*

iensis (Edmondson). Whether it is distinct from Coutière's inadequately described and figured specimen cannot be ascertained until the type specimen is redescribed. It is distinguished from *S. hilarula* by a longer scaphocerite, which in *hilarula* reaches only to the end of the second antennular article, and by different shape in the orbital teeth and different proportions in the third legs. *S. mauiensis* does not have the trapeziform notch in the telson, but has instead a shallow to almost nonexistent "v" that reaches from corner to corner.

Salmaneus tafaongae sp. nov.

TYPE SPECIMEN: A fragmentary ovigerous female, carapace length 3.2 mm, total length 8.8 mm, collected on outer portion of fringing reef, shoreward of surf zone, about one ft below low water, 3 miles east of Apia, Upolu, Western Samoa; collected by A. H. Banner, 24 April 1954.

DESCRIPTION: Body slender and relatively elongate for shrimp of this genus. Rostrum triangular, elongate, 3 times as long as broad at base (base considered as at end of straighter portion of margins); margins with only slight concavity anterior to eyes; tip acute, reaching almost to end of antennular article, bearing small tooth. Supracorneal spines acute, upturned, reaching half the length of visible portion of first antennular article. Corneas visible dorsally between supracorneal spines and rostrum, and most of corneal hemisphere visible laterally. Anterior carapace without trace of carinae or grooves.

Antennular peduncle elongate, with second article about 1.3 times as long as broad, subequal in length to third article and shorter than first. Stylocerite acute, reaching to end of second antennular article. Secondary ramus of upper flagellum short and bearing numerous heavy setae. Basicerite bearing slight superior and stronger inferior teeth. Scaphocerite not reaching to end of third antennular article; squamous portion broadly rounded, slightly exceeding lateral spine in length. Carpocerite short, not reaching to middle of second antennular article.

Large chela lacking. Small chela with form typical of small chelae in *Salmaneus*, with ratio

of articles (starting from ischium) as 10:10:11:10:3 (the last two ratios referring to palm and fingers, respectively).

Carpus of second legs with first article 5 times length of second, second slightly shorter than fifth, third and fourth subequal and shorter than second.

Third to fifth legs elongate and slender. Ischium of third leg 5 times as long as broad, 0.66 as long as merus, and armed with two movable spines; merus 6.7 times as long as broad, unarmed. Carpus 0.8 length of merus, almost 10 times as long as broad distally, distally armed with movable spine on inferior margin. Propodus slightly longer, slightly thinner than carpus, bearing three slender spines on inferior margin, with the longest spine distal. Dactylus simple, slightly curved, tip acute, 7 times as long as broad at base, half the length of the carpus, and bearing a tuft of fine setae two-thirds of distance to tip. Brush on fifth legs poorly developed.

Telson 5.6 times as long as posterior margin is broad, 2.6 times as broad anteriorly as posteriorly; posterior cleft trapeziform, narrow, and shallow; terminal spines heavy, middle pair 1.6 times as long as posterior margin is broad; cleft bearing single pair of setiferous bristles; dorsal spinules slight. Uropods slender, longer than telson; tooth on outer uropod heavy, reaching to end of squamous portion.

DISCUSSION: It was unfortunate that this single specimen was not more nearly intact, and that the small chela and second legs were lost after the initial examination. However, because its form is so distinctive we have decided to describe it as a new species.

All of the characteristics available—the general body form, the development of the rostrum and supraorbital teeth, the form of the smaller chela, and the form of the telson—indicate that the species belongs to the genus *Salmonius*. It also lacks the anal tubercles and has the articulated pleura of the sixth abdominal segment, as is characteristic of *Salmonius*, and it has a branchial formula (5-1-8) of the genus. But without the final confirmation that can be obtained only from examination of the large chela, this assignment to genus must be provisional.

Within the genus it is similar to no species

in that the rostrum is so much longer than broad, in the exposure of the corneas dorsally and laterally, in the angle of the orbital teeth, and in the extreme elongation of the third legs. While the form of the posterior notch of the telson and the lack of carinae on the carapace is similar to *S. sibogae*, not enough is known about the members of this genus to hazard a guess as to interspecific relationship.

This species is named in honor of Miss Tafaonga Uitime (now Mrs. Stewart), then a school teacher at Vailutai, Upolu, who served as an interpreter in the village and arranged for helpers and outrigger canoes during the collecting there.

ALPHEOPSIS Coutière

Alpheopsis equalis Coutière

For full citation see Banner and Banner (1960:86).

LOCALITIES: Fiji: 3 specimens from BF 13; 1, BF 16; 3, BF 17. Tonga: 1 specimen from BT 17. Samoa: 2 specimens from BAS 6; 1, BAS 7; 1, BAS 8; 2, BAS 9; 4, BAS 13; 1, BBS 1; 4, BP 8; 1, BP 13.

Alpheopsis species

Related to:

Betaeus trispinosus Stimpson, 1860. Acad. Nat. Sci. Philadelphia, Proc. 12:32.

Alpheopsis trispinosus Hale, 1941. Rep. B. A. N. Z. Antarct. Exped. 4(9):266, fig. 4.

Alpheopsis species de Man, 1922. Siboga Exped. 39a⁴(5):24, pl. 3, fig. 12.

LOCALITY: 1 fragmentary specimen from Samoa.

DISCUSSION: Because this specimen, the only one of this species in the collection, has only one third and one fourth leg intact posterior to the maxillipeds, it cannot be identified except tentatively. However, in those parts which are intact it agrees well with both Stimpson's original description, with Hale's short note, and with the description of *Alpheopsis* species by de Man. The chief difference between this specimen and that described by de Man is that in this one the telson is 3.5 times as long as the posterior margin is broad, and de Man states

that in his the ratio is 10:1. However, if the figure stated by de Man is correct then his specimen must have had an extremely attenuated telson; it is possible that his ratio may have been in error.

The identity of *A. trispinosus* needs to be established by the description of a neotype. Stimpson's description, while more full than those of many later workers, is so ambiguous that the identity of his species is questionable. His type came from Port Jackson, Sidney, Australia; yet Coutière (evidently with only Atlantic specimens) published many figures of what he believed to be this species. Because Coutière's drawings and descriptions of the Atlantic specimens did not agree perfectly with a single broken, and possibly immature, Indonesian specimen, de Man did not use the name *A. trispinosus*. It is not known whether our specimen from Samoa, de Man's from Indonesia, Hale's from Tasmania, and the specimens from the Atlantic are or are not the same species.

On the basis of the distributional patterns common in the family, it is likely that the specimens described by Stimpson and Hale represent a temperate Pacific species, that this specimen from Samoa and the specimens of de Man from Indonesia are a tropical Pacific species, and finally that the specimens of Coutière and Sollaud from the tropical and subtropical Atlantic represent a third species. Holthuis (1951:94) expressed similar doubts about the identity of the Atlantic species with the Pacific species, although he accepted Hale's hesitant view that de Man's and Stimpson's specimens are of the same species. Obviously no certain identification can be made until many more complete specimens from the various parts of this supposed range are studied.

Alpheopsis diabolus Banner

Alpheopsis diabolis Banner, 1956. Pacific Sci. 10(3):325, fig. 3.

Alpheopsis diabolus Banner and Banner, 1964. Pacific Sci. 18(1):86.

LOCALITY: Fiji: 1 specimen from BF 20.

SYNALPHEUS Bate

Synalpheus streptodactylus streptodactylus
Coutière

Synalpheus neomeris streptodactylus
Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):870, pl. 70, fig. 1.

Synalpheus streptodactylus de Man, 1911. Siboga Exped. 39a¹(2): 226, pl. 7, fig. 29.

Synalpheus metaneomeris streptodactylus
Coutière, 1921. Linn. Soc. Zool., Journ. 17(4):414.

LOCALITIES: Tonga: 1 specimen from BT 1; 1, BT 6; 7, BT 7; 2, BT 9. Samoa: 1 specimen from BAS 10; 27, BBS 27.

DISCUSSION: Coutière in 1905 described a form of *Synalpheus* to which he gave the varietal name *Synalpheus neomeris streptodactylus*; this he distinguished primarily by differences in the dactyli of the pereopods. In 1911 de Man reported that he had examined the types of Coutière's variety as well as a group of related specimens collected by the Siboga Expedition. He found that Coutière's variety was specifically separate from *S. neomeris* on the basis of a series of characteristics which included the proportions of the antennular peduncles, the chelae, the walking legs, and the telson; for his new species he retained the name *S. streptodactylus*.

However, Coutière (1921:414), in reporting additional specimens, accepted de Man's specific separation but stated that there were actually two varieties involved—those with the dactylus of the walking leg as he originally described it, and those with a heavier ventral unguis. Because he accepted the concept that both of these varieties were of a species separate from *S. neomeris*, he proposed to give the name *S. meta-neomeris* for the species, retaining the name *S. m. streptodactylus* only for those with the modified dactylus.

This action by Coutière is a violation of the rules of nomenclature. When a named variety or subspecies is raised to specific rank it must continue to bear the name originally assigned; if the new species be divided into subspecies, the subspecies that contains the types for the species bears as a subspecific name the duplicated specific name, and the differing subspecies bears a new name. Therefore the correct name of this species is *S. streptodactylus* Coutière; the subspecies originally described by Coutière must be *S. streptodactylus streptodactylus*, and the

subspecies with the other type of dactylus must bear a new name. For this subspecies the name *metaneomeris* is not available, as it was attached by Coutière to the type for *S. streptodactylus* and is a synonym. Therefore we here give to the subspecies described and named by Coutière as *S. metaneomeris streptodactylus* (1921:414) the new name of *S. streptodactylus hadrungus* (from the Greek *hadros*, thick).

The difference between the two subspecies lies in the proportions of the ungui of the dactylus of the walking legs. In *S. s. streptodactylus* the ventral hook is 2.5–3.6 times as long as thick at its base, its base is twice that of the dorsal, and its length is 1.5 that of the dorsal; in *S. s. hadrungus* the latter proportions are 2.0 and 3.6. (The proportions of the ventral hook alone were not reported, but, according to Coutière's 1921 figures, it should be about 2.5 times as long as thick.) In spite of this slight and subtle difference, and in spite of the variation in proportions usually found in this family and genus, none of the specimens in our collection was intermediate between two subspecies. In these specimens the range of proportions on the diagnostic characteristics are as follows (15 specimens from 4 localities were measured; the average measurements are given in parentheses): ventral hook, length—breadth, 1.7–3.0, (2.2); length ventral hook—length dorsal hook, 1.0–1.2, (1.1); thickness ventral hook—thickness dorsal hook, 1.7–2.0, (2.0). Therefore all of our specimens are *S. s. streptodactylus*.

Since the paper dealing with the additional reports on the Hawaiian alpheidids appeared we have discovered *S. s. streptodactylus* in Hawaii. Here the species is abundant on the spongocoel of a large sponge, *Zygomyscale parishei* (Bowerbank) (de Laubenfels, 1950: 25). Previous reports on the species do not note any association with sponges, and if the non-Hawaiian specimens in the collection were associated with a sponge, the sponge was not a distinct massive sponge but was one found in the branches of dead coral heads.

Synalpheus paraneomeris Coutière

For full citation see Banner and Banner (1964:86).

LOCALITIES: Fiji: 19 specimens from BF 16; 1, BF 19; 7, BF 21. Tonga: 1 specimen from BT 9; 6, BT 10; 1, BT 11; 2, BT 17. Samoa: 2 specimens from BAS 5; 1, BAS 7; 1, BAS 9; 1, BAS 10; 1, BAS 13; 2, BBS 6; 1, BBS 7; 1, BBS 8; 8, BBS 11; 2, BP 4; 6, BP 8; 1, BP 13; 12, BP 16.

Synalpheus hastilicrassus Coutière

Synalpheus hastilicrassus Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4): 875, pl. 72, fig. 12.

LOCALITIES: Fiji: 1 specimen from BF 8; 1, BF 14; 1, BF 18; 1, BF 20.

Synalpheus coutierei Banner

Synalpheus coutierei Banner, 1953. Pacific Sci. 7(1):36.

LOCALITIES: Fiji: 1 specimen from BF 7; 1, BF 8; 1, BF 11; 1, BF 14; 2, BF 16. Tonga: 2 specimens from BT 4; 4, BT 5; 1, BT 8; 2, BT 9; 2, BT 16. Samoa: 1 specimen from BAS 9; 2, BBS 7.

Synalpheus anceps Banner

Synalpheus anceps Banner, 1956. Pacific Sci. 10(3):334, fig. 8.

LOCALITIES: Fiji: 1 specimen from BF 7; 1, BF 13. Samoa: 1 specimen from BAS 12; 1, BBS 5.

Synalpheus laticeps Coutière

Synalpheus laticeps Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):874, pl. 72, fig. 11.

LOCALITIES: Samoa: 4 specimens from BBS 1; 3, BP 8.

Synalpheus charon charon (Heller)

Alpheus charon Heller, 1861. K. Akad. Wiss. Wien, Sitzung. 44:272.

Synalpheus charon charon Banner, 1956. Pacific Sci. 10(3):331.

LOCALITY: Samoa: 2 specimens from BBS 11.

Synalpheus nilandensis oxyceros Coutière

Synalpheus nilandensis oxyceros Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):871, pl. 70, fig. 5.

LOCALITY: Samoa: 1 specimen from BAS 9.

Synalpheus heroni Coutière

Synalpheus heroni Coutière, 1909. U. S. Nat. Mus., Proc. 36:42, fig. 24.

LOCALITY: Fiji: 1 specimen from BF 16.

Synalpheus tumidomanus (Paulson)

Alpheus tumidomanus Paulson, 1875. Invest. Red Sea Crust. (1): 101, pl. 13, fig. 2.

LOCALITY: Samoa: 1 specimen from BP 4.

ALPHEUS Fabricius

MEGACHELES GROUP

? *Alpheus lanceostylus* Banner

Alpheus lanceostylus Banner, 1959. Pacific Sci. 13(2):136, fig. 3.

LOCALITY: Samoa: 1 specimen from BAS 5.

DISCUSSION: This specimen is lacking both the large and small chelae, and cannot be assigned to this species with certainty. When compared with the type specimen for *A. lanceostylus*, no points of difference were found except for very slight differences in proportions; however, it also agrees quite well with *A. edmondsoni* (Banner). The specimen has been placed in this species because it has a slightly thicker antennular peduncle than is normal for *A. edmondsoni*.

Alpheus collumianus medius Banner

Alpheus collumianus medius Banner, 1956. Pacific Sci. 10(3):340, fig. 11.

LOCALITIES: Fiji: 1 specimen from BF 12; 4, BF 13; 6, BF 15; 1, BF 16; 1, BF 20. Tonga: 1 specimen from BT 9; 4, BT 10; 13, BT 11; 3, BT 13. Samoa: 1 specimen from BAS 3; 1, BAS 6; 2, BAS 7; 2, BAS 9; 2, BAS 12; 2, BAS 13; 1, BBS 5.

Alpheus collumianus probabilis Banner

Alpheus collumianus probabilis Banner, 1956. Pacific Sci. 10(3):338, fig. 10.

LOCALITIES: Fiji: 1 specimen from BF 2; 1, BF 13; 2, BF 14; 2, BF 17; 3, BF 20. Tonga: 2 specimens from BT 9; 2, BT 12. Samoa: 1 specimen from BAS 4; 2, BAS 6; 5, BAS 9; 1, BAS 13; 3, BBS 5; 2, BBS 8; 2, BP 4; 2, BP 12; 2, BP 13.

Alpheus collumianus inermis Banner

Alpheus collumianus inermis Banner, 1956. Pacific Sci. 10(3):342, fig. 12.

LOCALITIES: Fiji: 2 specimens from BF 5; 1, BF 21. Samoa: 1 specimen from BAS 7; 15, BP 4.

Alpheus crockeri Armstrong

Crangon crockeri Armstrong, 1941. American Mus. Nov. (1137):8, figs. 2, 3.

Crangon tuthilli Banner, 1953. Pacific Sci. 7(1):63, fig. 19 a-d.

Alpheus tuthilli Banner, 1956. Pacific Sci. 10(3):338, fig. 9.

LOCALITIES: Samoa: 1 specimen from BAS 13; 4, BBS 3.

DISCUSSION: Careful comparison of the descriptions of *A. crockeri* and *A. tuthilli*, and of these specimens from Samoa with the specimens from Hawaii, leaves no doubt that *A. tuthilli* is a synonym.

Alpheus deuteropus Hilgendorf

Alpheus deuteropus Hilgendorf, 1878. Monats. Berlin Akad. Wiss. p. 834, taf. 4, fig. 8. Banner and Banner, 1964. Pacific Sci. 18(1):88.

Crangon deuteropus Banner, 1953. Pacific Sci. 7(1):70, fig. 22.

LOCALITY: Samoa: 1 specimen from BP 1.

MACROCHIRUS GROUP

Alpheus paragracilis Coutière

Alpheus paragracilis Coutière, 1897b. Paris Mus. Hist. Nat., Bull. 3(7):303.

LOCALITIES: Tonga: 1 specimen from BT 5; 6, BT 9; 17, BT 10; 17, BT 11; 10, BT 13; 12, BT 17. Samoa: 1 specimen from BAS 9; 7, BAS 12; 10, BAS 13; 3, BBS 6; 4, BP 6; 1, BP 8.

Alpheus clippertoni (Schmitt)

For full citation see Banner and Banner (1964:89).

LOCALITIES: Tonga: 4 specimens from BT 17. Samoa: 2 specimens from BAS 12; 2, BBS 11; 3, BP 4; 1, BP 16.

Alpheus macrochirus Richters

Alpheus macrochirus Richters, 1880. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164, taf. 17, figs. 31-33.

LOCALITY: Fiji: 1 specimen from BF 20.

Alpheus lottini Guérin

For full citation see Banner and Banner (1964:88).

LOCALITIES: Fiji: 3 specimens from BF 1; 1, BF 8; 3, BF 9; 2, BF 10; 1, BF 12; 2, BF 13; 2, BF 15. Tonga: 1 specimen from BT 5; 8, BT 9. Samoa: 6 specimens from BAS 2; 1, BAS 5; 6, BAS 10; 9, BAS 12; 2, BAS 14; 2, BBS 1; 1, BBS 7; 2, BBS 10; 2, BBS 11; 2, BP 1; 5, BP 11; 5, BP 13.

Alpheus gracilis Heller

Alpheus gracilis Heller, 1861. K. Akad. Wiss. Wien, Sitzung. 44(1):271, taf. 3, figs. 19-20.

LOCALITIES: Tonga: 1 specimen (collection data lost). Samoa: 3 specimens (collection data lost); 5, BP 8.

Alpheus acutofemoratus Dana

Alpheus acutofemoratus Dana, 1852a. U. S. Explor. Exped. 13: 550, pl. 35, fig. 2. De Man, 1902. Senckenb. Naturf. Gesell., Abhandl. 25:886, pl. 27, fig. 63.

nec Alpheus acutofemoratus Spence Bate, 1888. Challenger Rpts. 24:545, pl. 97, fig. 2.

Alpheus parabrevipes Coutière, 1898a. Soc. Ent. France, Bull. 1898(6):151, fig. 2.

LOCALITIES: Fiji: 2 specimens from BF 4. Tonga: 2 specimens from BT 8; 3, BT 9; 3, BT 12. Samoa: 2 specimens from BBS 1; 8, BBS 2; 1, BBS 7; 7, BBS 9; 1, BBS 10; 1, BP 3; 2, BP 9; 37, BP 14.

DISCUSSION: These specimens agree almost perfectly with the description given by de Man except that in only one does the small chela bear a trace of the longitudinal groove he described, and the second carpal article of the second legs is usually about 3 times the length of the first, instead of about 2.5 times as long. Possibly also the large and small chela bear more dense hair, but de Man's description is a little ambiguous on that point.

Alpheus tungii sp. nov.

TYPE SPECIMEN: A male 15.5 mm long (carapace length 5.5 mm) collected from the south coast of Tongatabu, Tonga, in head of dead and overgrown *Acropora*, at outer edge of fringing reef near surge channel, on March 31, 1954 by A. H. Banner. Only specimen known.

DESCRIPTION: Body sturdy and covered on almost all parts, including the carapace, abdominal terga, dorsal side of telson, and larger appendages, with scattered fine setae; setae nowhere dense enough to obscure form of exoskeleton.

Anterior portion of carapace bearing a low rounded medial crest extending from tip of rostrum to middle of carapace, carina not bearing tooth. Rostrum triangular with concave margins, tip reaching about two-thirds length of first antennular article; lateral margins bearing three strong setae; rostrum and anterior carapace depressed when seen in lateral view. Orbital hoods inflated, rounded, demarked from surrounding carapace, and carrying on medial surface, above frontal edge of carapace, strong teeth which reach about half length of rostrum. Orbital hoods bearing setae only around margins, hood not fully transparent because of scattered opaque limy spots (in preservative); eyes black, of normal size and development.

Stylocerite short, broad, with tip of tooth not reaching beyond end of first antennular article. Second antennular article with low rounded lateral crest; article 1.5 times as long as broad, about equal in length to basal article, and 1.4 times length of distal article. Basicerite heavy with strong lateral spine reaching beyond middle of second antennular article. Scapho-

cerite with acute, narrow tip extending considerably beyond end of antennular peduncle; lateral margin curved, proximally provided near articulation with strong tooth at right angles to margin; squamous portion short and narrow reaching only slightly beyond end of second antennular article. Carpocerite equal in length to scaphocerite.

Middle article of third maxilliped with strong rounded projection on inferior external margin.

Merus of large cheliped less than 0.3 length of chela; superior margin projecting but not acute; inferior internal margin with several slight rounded protuberances and bearing short, soft setae and two short spines distally; article otherwise without setae except on superior distal margin. Chela heavy, compressed, 2.1 times as long as broad at maximum breadth, with fingers occupying only distal 0.2 of entire length.

Palm with sharply delimited superior groove extending full length of chela; superior crest terminating in heavy rounded projection above dactylar articulation. Projection especially conspicuous on inner face. Plaque crest flat, margins sharp, terminating in two rounded teeth flanking adhesive plaque. Palmar groove shallow but well delimited distally. Inferior crest flattened, ending in small acute tooth. Inferior depression rounded. Dactylar articulation also flanked with strong tooth on superiomedial side. Dactylus heavy and rounded. Upper portion of superiomedial face papillose, papillae bearing short and mostly light setae; other portions of chela with at most scattered setae; chela not conspicuously hirsute.

Small cheliped heavy. Superior margin of merus projecting distally into low rounded tooth; inferior internal margin armed with three small spines carried on heavy protuberances. Carpus with superior distal margin projecting as strong tooth over base of chela. Chela 3 times as long as broad, with fingers occupying distal 0.45. Palm with superior groove and crest similar to those of large chela, except shallow and poorly developed; superior crest projecting above dactylar articulation as small, acute tooth; opposite margin of dactylar articulation bearing similar but smaller tooth; superior and internal surface of palm papillose with papillae bearing heavy but not long setae. Fingers heavy, with

dactylus slightly curved and fixed finger bearing cutting flange on internal edge; tips hooked, pointed, and crossing.

Carpal articles of second leg with ratio: 10:4.1:3.0:2.6:9.9.

Third leg with ischium bearing heavy movable spine; merus 2.9 times as long as broad, inferior margins bearing a series of setiferous notches and strong terminal tooth; carpus 0.56 as long as merus, with superior margin bearing setae and both superior and inferior margins projecting distally into acute teeth; propodus 0.75 as long as merus, bearing setae on superior margin and five pairs of spines on inferior margin and two on terminal margin; dactylus curved, 0.27 as long as merus, biunguiculate with lower unguis small.

Outer uropod with strong lateral spine; inner uropod with a series of strong movable spines. Telson 2.7 times as long as broad posteriorly, 1.5 times as broad anteriorly as posteriorly; lateral margins almost straight, posterior margin shallowly arcuate; dorsal and terminal spinules of moderate size.

DISCUSSION: This species belongs to the *Macrochirus* group, and within the group it is obviously most closely related to *A. villosus* (Olivier). Like *A. villosus* this species has hairs over the body surface, a carinate carapace, orbital teeth, a strong spine on the basiscerite, grooves and teeth on the large chela, an acute tooth on the merus, and a biunguiculate dactylus on the third legs, etc.

Without a full description of *A. villosus*, point for point comparisons are difficult. The differences between the illustrations of Coutière (1899, *seriatim*), taken from Olivier's type, and Bate's drawings of *Paralpheus diversimanus* (Olivier) (Chall. Rept., pl. 102, fig. 1), which Coutière states is identical with *A. villosus* (1898b:204), are especially confusing. Without any actual specimens of *A. villosus* for comparison, we have presumed the drawings and fragmentary description of Coutière to be more accurate and have used them as much as possible in Table 2.

There is evidently a difference in the large chela, especially around the articulation of the dactylus, but Coutière's sole figure (1899:220, fig. 266) is difficult to interpret.

Other species given by Coutière as being related to *A. villosus* can be separated by a number of characteristics. *A. malleator* Dana differs in the form of the rostrum and orbital hoods and in the large chela; *A. rugimanus* A. Milne-Edwards differs in the large chela; *A. socialis* Heller lacks the tooth on the merus of the third legs; and *A. macrochirus* Richters lacks the orbital teeth and differs in the form of the large chela.

This species has been named in honor of Prince Tungi of the Kingdom of Tonga, who was most cooperative during the field work on Tongatabu.

OBESOMANUS GROUP

In the *Obesomanus* group a large number of species have been described based upon few specimens; as in other groups rather subtle differences in form of rostral front and chelae, and slight to major differences in proportions of articles have been used as criteria for the differentiation of the species. Inasmuch as it has become apparent in the study of our collections, which contain relatively large numbers of some species, that these species are possibly the most variable of all the species of *Alpheus*, we have decided to study the extent of variation in characteristics used as criteria to separate the described species.

This paper has been chosen as the logical one

of the series in which to discuss this variation and to evaluate the validity of the Indo-Pacific species placed in this group. For this study all of the specimens in the collections available, those already reported, those reported in this paper, and those to be listed in future papers, were carefully examined.

Of the numerous species attributed to this group we now recognize only six in our Central Pacific collections: *A. obesomanus* Dana, *A. malleodigitus* (Bate), and *A. microstylus* (Bate), all with numerous specimens, and *A. perplexus* Banner, *A. chamorro* Banner, and *A. samoa* (described below) with but few specimens. In our reconsideration of the group we have decided that the genus *Thunor* is not valid and we have placed its species also within the *Obesomanus* group, thereby adding two more central Pacific species, *A. idiocheles* Coutière and *A. microscaphis* (Banner).

In only the first three species could variation be studied. For these three species samples were compared from all parts of the range represented. Because no significant differences were found from one locality to another, figures on their variations were combined. A total of 80 specimens of *A. obesomanus*, 87 specimens of *A. malleodigitus*, and 9 specimens of *A. microstylus* (all of them reasonably intact) were measured. To show the normal form of the three species, the anterior body region and the

TABLE 2

DIFFERENTIATING CHARACTERISTICS OF *A. villosus* AND *A. tungii*

<i>A. villosus</i>	<i>A. tungii</i>
1. Median crest of carapace bearing tooth posterior to the orbital hood.	1. Median crest without tooth.
2. Secondary teeth between orbital teeth and rostrum.	2. Secondary teeth lacking.
3. Orbital hoods covered with an enmeshment of hairs ("entrêmelées de poils") and corneas of eyes "dépigmentées et de couleur crayeuse."	3. Orbital hoods with hair light and scattered; corneas of normal pigmentation.
4. Third leg with carpus armed with 5 movable spines and only slight superior distal tooth; propodus armed on inferior margin with over 8 pairs of spines; secondary unguis of dactylus heavy.	4. Third leg with carpus lacking movable spines, superior distal tooth heavy; propodus with 5 pairs of spines; secondary unguis of dactylus slight.
5. Inner uropod with outer distal margin unarmed.	5. Inner uropod with outer distal margin bearing a row of movable spines.

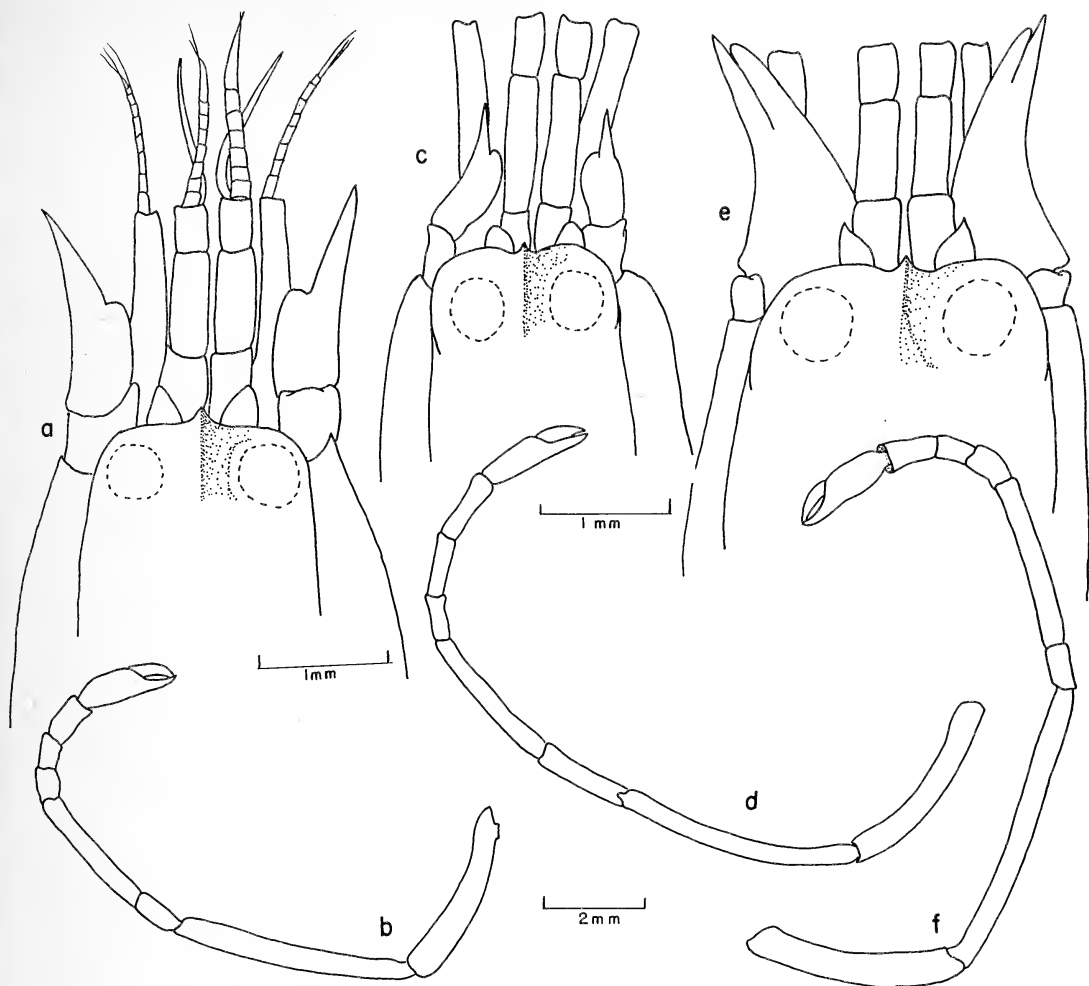


FIG. 8. *Alpheus obesomanus* Dana. 18 mm male from station BP 10. *a*, Anterior body region; *b*, second leg. *Alpheus malleodigitus* (Bate). 20 mm male from station BP 4. *c*, Anterior body region; *d*, second leg. *Alpheus microstylus* (Bate). 23 mm male from station BP 13. *e*, Anterior body region; *f*, second leg.

second leg are presented in Figure 8.

Orbital hoods and rostral front. As previously reported the anterior body region is variable; the rostrum itself in all three species is present, but may be exceedingly minute (de Man and Coutière both reported specimens in which it was lacking); and the frontal margin of the carapace between the orbital hoods varies from straight to bent inwards towards the rostrum.

Antennular peduncles (Figs. 9 and 10). No sexual dimorphism was found in this characteristic; therefore figures for male and female

were combined. The curves for the relative lengths of the first and second antennular articles show that while there is a statistical difference between *A. obesomanus* and *A. malleodigitus* there is so much overlap that the characteristic cannot be used for species differentiation; *A. microstylus* also falls within the same range. The length-breadth ratio of the second article shows a greater contrast between *A. obesomanus* and *A. microstylus* on one hand and *A. malleodigitus* on the other, but again the difference is not clear-cut. It will be noted that in the wide variation in these characteristics

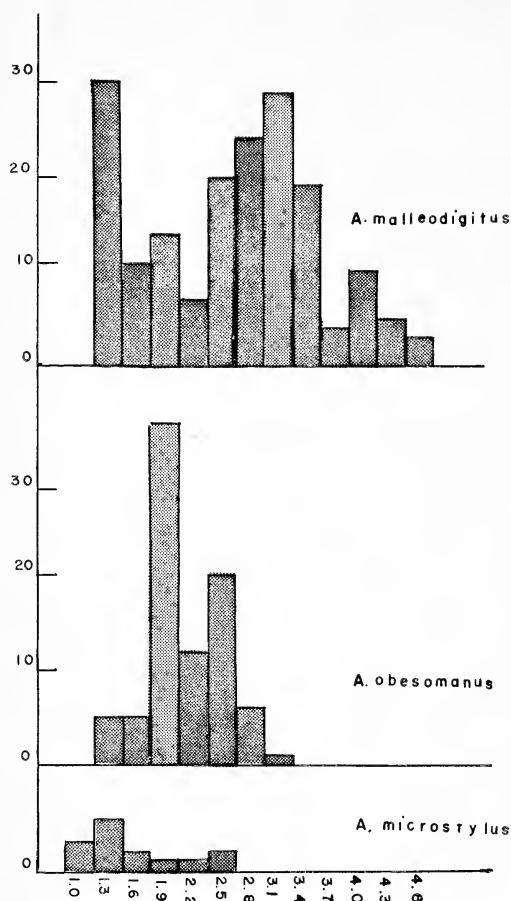


FIG. 9. *Obesomanus* group; variations in proportions of antennular articles in three species. *Ordinate*: length of second article divided by length of first article. *Abcissa*: number of specimens.

attributed to *A. malleodigitus* there appears to be a bi- or even tri-modal curve which could indicate two or three separate species with overlapping variation; however, in careful correlation with other characteristics we could find no related differences that could separate these groups. Therefore, we have interpreted this as a probable difference in geographically separated populations.

Antennal peduncle (Figs. 11, 12, and 13). In this appendage there is a clear differentiation between *A. obesomanus* and *A. malleodigitus* in the relative lengths of the scaphocerite and carpoperite when compared with the antennular articles, the scaphocerites being definitely shorter in the latter species; *A. obesomanus* and

A. microstylus, similar in their carpoperites and scaphocerites, are differentiated by the lengths of the squamous portion. In *A. microstylus* the squame reaches to near the end of the third, and in *A. obesomanus* it reaches only to the middle of the second antennular article.

Large chela. On this appendage emphasis has been made on the degree of sculpturing. In most specimens the chitin of the body of the chela is relatively soft, being stiff only where muscles or ligaments are attached; as a consequence the process of preservation alters the extent of the depressions and grooves, and no great significance should be attached to either their depth or breadth. However, all had some indentations, and none closely approached the smooth condition reported by Dana for his species *A. obesomanus* (his drawing appears to be of the medial face, which is smooth in most species of this group).

Small chela (Fig. 14). This characteristic has been used by de Man (1911:313) as a distinguishing characteristic in his key ("fingers of small chela of the male much shorter than palm, the proportion between the length of the

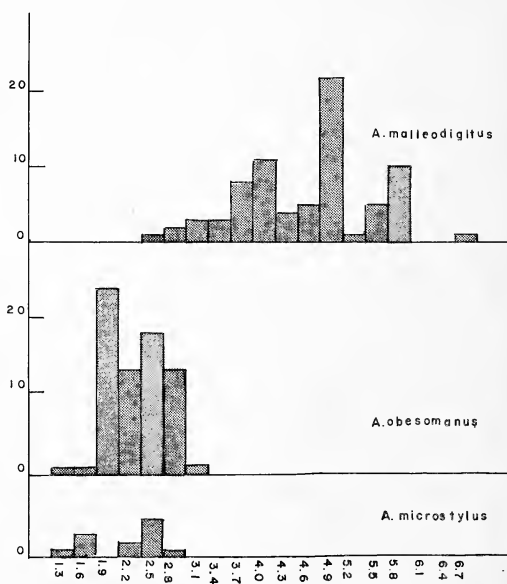


FIG. 10. *Obesomanus* group; proportions of second antennular article in three species. *Ordinate*: length of second antennular article divided by its breadth. *Abcissa*: number of specimens.

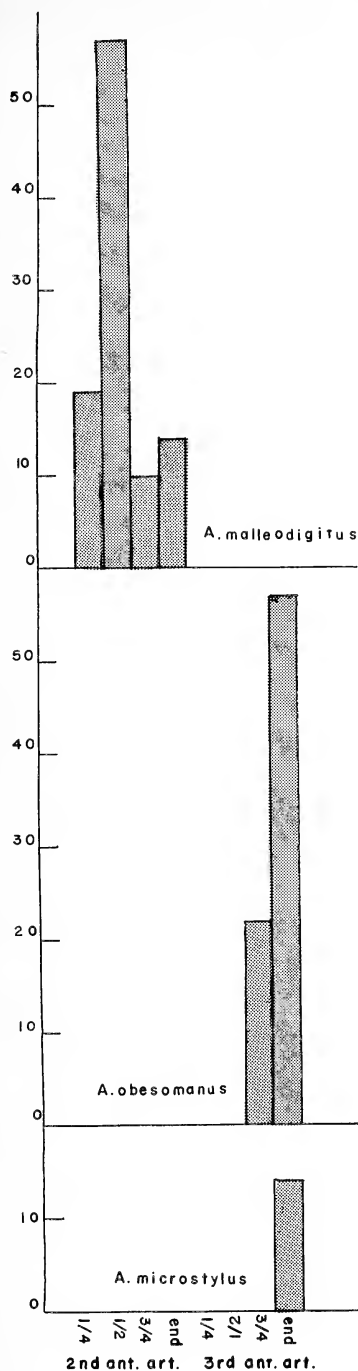


FIG. 11. Obesomanus group; relative proportions of scaphocerite and antennal peduncle in three species. Ordinate: length of scaphocerite in relation to second and third antennular article. Abcissa: number of specimens.

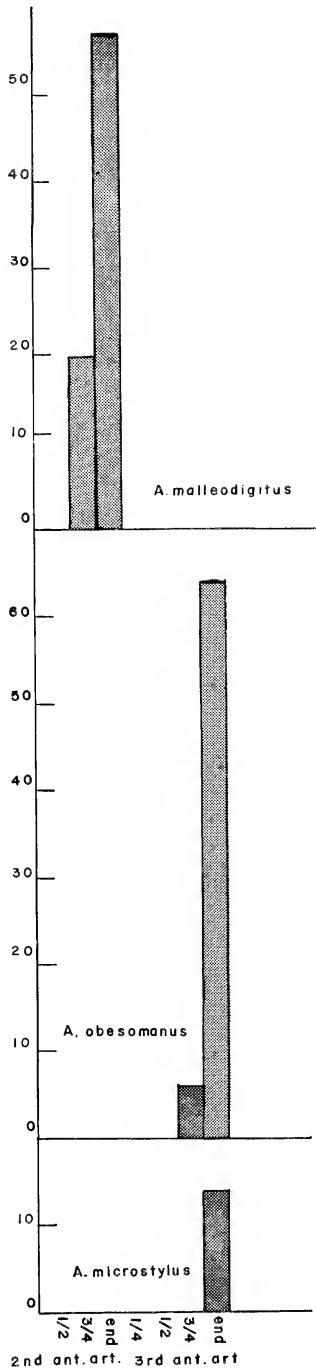


FIG. 12. Obesomanus group; relative proportion of the carpocerite to the antennal peduncle in three species. Ordinate: length of carpocerite in relation to second and third antennular peduncle in three species. Abcissa: number of specimens.

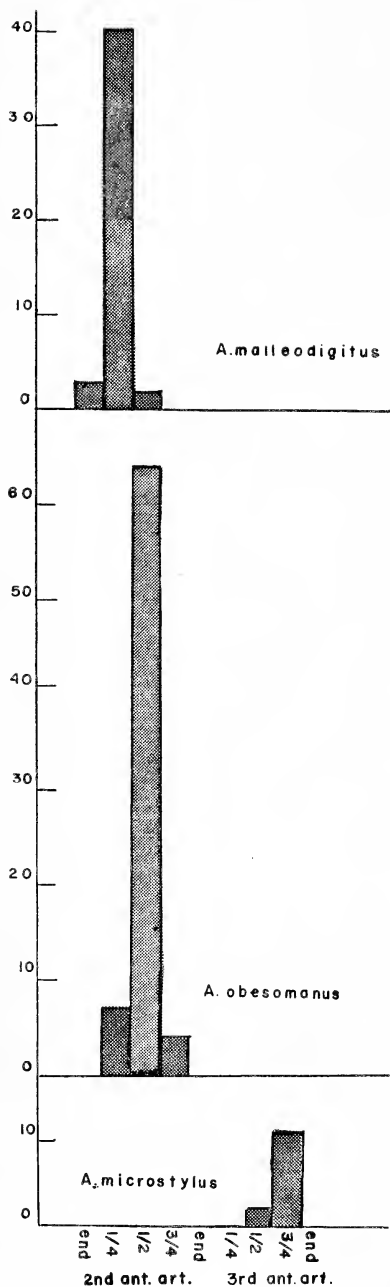


FIG. 13. Obesomanus group; relative proportions of the squame to the antennal peduncle in three species. Ordinate: length of squame in relation to the second and third antennular article. Abcissa: number of specimens.

chela and that of the fingers more than 3 as opposed to a little shorter than the palm. . . less than 3"). The graphs show that, while there may be statistical differences, this characteristic cannot be used for separation of individual specimens. Analysis showed no differences between the sexes, and so these are not differentiated on the graph.

Second leg (Fig. 15). Between the two species, *A. malleodigitus* and *A. obesomanus*, the characteristic that seems to give the best differentiation is the ratio of the first two carpal articles: in *A. malleodigitus* the ratio is less than 1:2 (usually about 1:1.5), while every specimen of *A. obesomanus* has a ratio of more than 1:2 (usually about 1:3). The few specimens of *A. microstylus*, however, seem to fall into the range of *A. obesomanus*.

Third leg (Figs. 16 and 17). In these the length-breadth relationship of both the merus and the carpus are graphed and no sharp differentiation is found.

Telson (Fig. 18). When the length of the telson is contrasted with the breadth of the tip, a measurement often used in this genus as a specific characteristic, extreme variation is noted; it is doubtful if this should ever be used as a characteristic within this group.

With this knowledge of the variation in these three species, the separation of the Indo-Pacific species and varieties has been reviewed. The characteristics of those species not represented in the collection were derived entirely from the literature. These species are listed in the order of their consideration in the section which follows.

- A. obesomanus japonicus* Ortmann, 1890:478.
- A. microstylus* (Bate), 1888:566, pl. 101, fig. 6; Coutière 1899: Figs. 270-272, 400 (listed as *A. obesomanus* or *A. malleodigitus*); Coutière, 1905:884, pl. 76, fig. 23; de Man, 1911:344.
- A. microstylus* var ? de Man, 1911:345, pl. 14, fig. 68.
- A. lutini* Coutière, 1905:885, pl. 76, fig. 24; de Man, 1911:346, pl. 14, fig. 69.
- A. species 2* Banner, 1956:351, fig. 15.

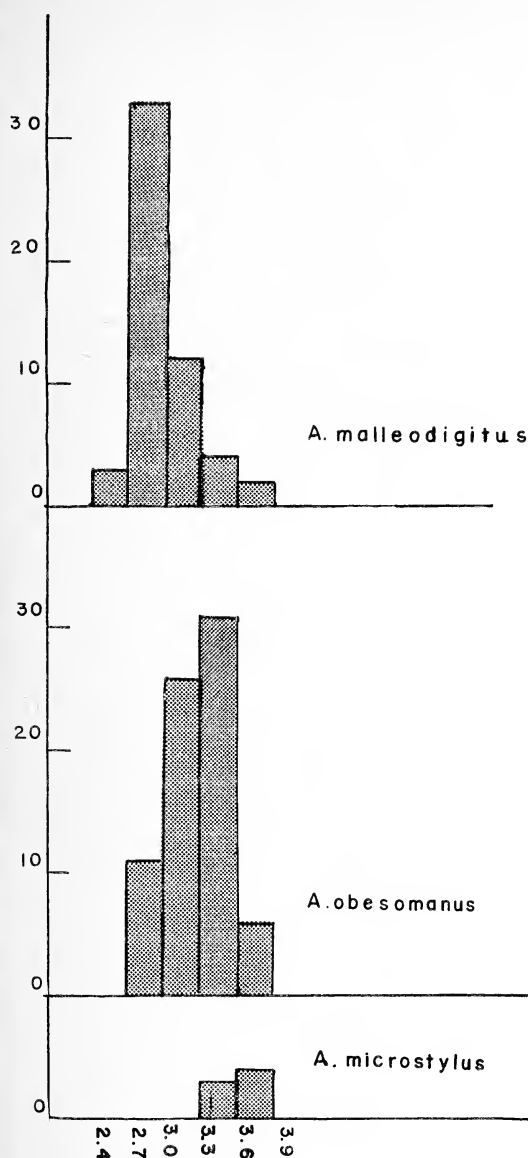


FIG. 14. Obesomanus group; relative proportions of the palm and fingers of the small chela of three species. Ordinate: ratio of the length of fingers to length of palm, the fingers being considered as 1. Abcissa: number of specimens.

A. malleodigitus (Bate), 1888:565, pl. 101, fig. 5; de Man, 1902:866; de Man, 1911:347, pl. 14, fig. 70–70d.

A. malleodigitus var. *gracilicarpus* de Man, 1909b:99; 1911:349, fig. 70.

A. phrygianus Coutière, 1905:886, pl. 77, fig. 25.

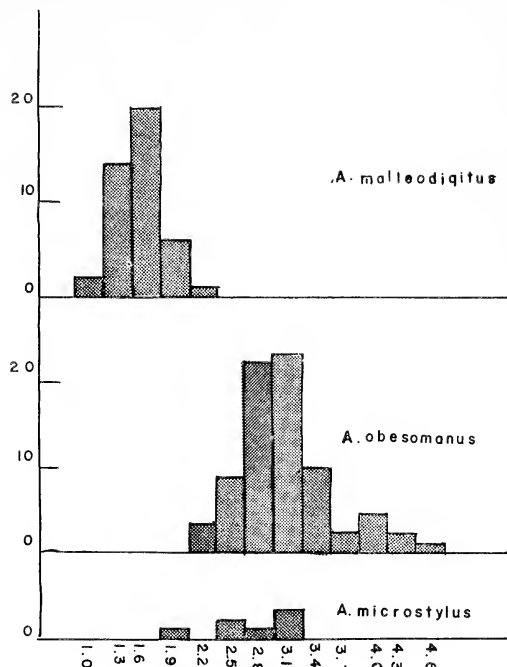


FIG. 15. Obesomanus group; proportions of first and second article of the second leg in three species. Ordinate: length of the second article of the second leg divided by the first. Abcissa: number of specimens.

A. danae Coutière, 1905:887, pl. 77, fig. 26.

A. persicus Nobili, 1906:33.

A. samoa (below).

A. species Nobili, 1906:34.

A. perplexus Banner, 1956:349, fig. 14.

A. species de Man, 1911:349, pl. 15, fig. 71.

A. chamorro Banner, 1956:349, fig. 14.

In addition to those species previously placed in the Obesomanus group, we are adding those species previously placed in *Thunor*, the relegation of *Thunor* to synonymy being discussed under *A. samoa* (below). These species are:

A. rathbunae (Schmitt), 1924:74, pl. 1, figs. 1–10. (Originally described as *Crangon rathbunae*, and later placed in the genus *Thunor*.)

A. idiocheles Coutière, 1905:883, pl. 75, fig. 21. Later named *Thunor idiocheles* [Coutière] (Banner, 1956:367, fig. 22).

A. baculifer Coutière, 1908:16.

A. microscaphis (Banner), 1959:151, fig. 13.

In the summation of the characteristics of the species given below, the original description was used wherever possible; for some characteristics, especially proportions, the original figures were used; only where both of these were insufficient were the later redescrptions used (of the type or supposedly similar specimens). The species have been divided into four groups for the purpose of this discussion:

I. Those species with a strong articulation of the outer uropod.

A. Those with simple dactyli on the posterior legs, and with elongate second articles in the carpus of the second legs.

1. *A. obesomanus* Dana. This species, the first one described in the group, was characterized by having the second article of the antennular peduncle 1.5 times the length of the first, and 3 times as long as broad; the scaphocerite and the carpocerite barely reaching to the end of the second antennular article, and the squamous portion of the scaphocerite reaching to the middle of the second antennular article (according to Boone, 1935); the large chela smooth (although Boone described depressed areas); the palm of the small chela

was described as 3 times as long as the fingers but illustrated as 2.5 times as long; the first two carpal articles of the second leg with the ratio of 1:4. (Dana's figures show a ratio of about 1:3.4 with the merus of the third leg armed, the dactylus simple.)

This species, the most common one in our collections, was identified originally in this series of papers as *A. lutini* Coutière (for characteristics see below), since almost all the specimens had longer scaphocerites and carpocerites than those described by Dana (Figs. 11 and 12). However, a few specimens of those measured approached the described condition of *A. obesomanus*, and other individuals not in the sample measured showed a gradation between these and the condition described by Dana. Of seven specimens in a single collection from Tahiti (BD 13), one has the scaphocerite and carpocerite not quite reaching to the tip of the second antennular article; one specimen has them reaching to the end of this article; in two the parts reach to the first quarter of the third antennular article; and in another two, to the middle of this article; in the remaining specimens they reach almost to the tip of the article.

This leaves the ratio of fingers to palm of the small chela as means of distinguishing between the two nominal species. These ratios were reported to be 1.0:2.5 in *A. obesomanus* and 1:1.5 in *A. lutini*. However, Dana's figures show a ratio of 1:2.5, and the measured specimens show a ratio of 1:1.5 to 1:2.5. Thus there is no differentiation. Other characteristics set forth by Coutière are also bridged by the variation reported above.

A neotype should be established from Fiji for this species, but all of the Fijian specimens at hand were more like the form described for *A. lutini* and none closely approached the characteristics given by Dana.

2. *A. obesomanus japonicus* Ortmann. Ortmann's original description is very inadequate to characterize this species. The second antennular article is more than twice as long as the first; the scaphocerite is "sehr schmal, fast so lang wie die Stiele der äusseren, kürzer die der inneren Antennen." The fingers of the small

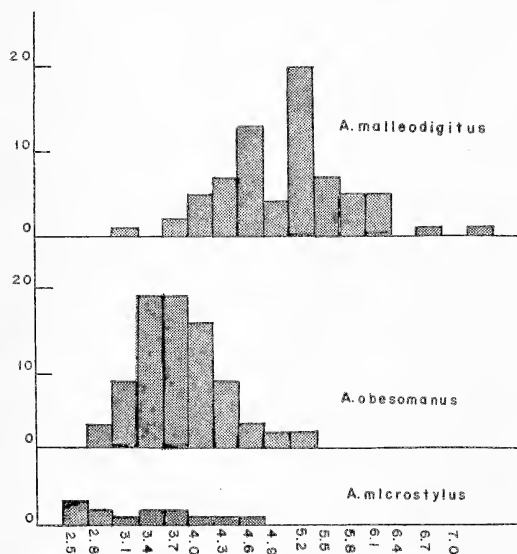


FIG. 16. *Obesomanus* group; proportions of the carpus of the third leg of three species. Ordinate: the length of the carpus of the third leg divided by the breadth. Abscissa: number of specimens.

chela are "somewhat shorter" than the palm; the second carpal article of the second leg is twice as long as the first.

This may be a distinct species, but because the only characteristic that is definitely stated is the relative length of the second carpal article, and as this relative length lies merely on the extreme margin of the normal curve for the supposed parent species (see Fig. 15), the subspecies must be regarded as indistinguishable from *A. obesomanus*.

If later study shows this to be a distinct species or subspecies the name will have to be changed, as Courière (1905:886) has already remarked, because the name *A. japoni-*

cus has already been used by Miers (1879:53) for a species in the *Edwardsii* group.

3. *A. microstylus* (Bate), when compared with *A. obesomanus*, appears to have slightly shorter and thicker second articles in the antennular peduncle 1.2 times the length of the first, and 2 times as long as broad. Most important, the end of the scaphocerite and carpoperite reach beyond the end of the antennular peduncle, and the squamous portion of the scaphocerite reaches almost to the end of the third article; the sculpturing of the large chela is deep and pronounced, and the palm of the small chela varies from 1.5 to 2.1 times the length of the fingers; the first two carpal articles of the second legs bear the ratio of 1:3, the third legs are similar to those of *A. obesomanus* and vary from 3.0 to 4 times as long as broad. There seems no doubt that this species is valid and distinct from *A. obesomanus*, as shown by the differences in the antennal peduncle, small chela, and second legs; it is probable that the differences in the large chela are constant and discernable as well.

4. *A. microstylus* var? de Man. This possible variety was separated by de Man from the parent species solely on the basis of the thinner second segment of the second legs, 9–14

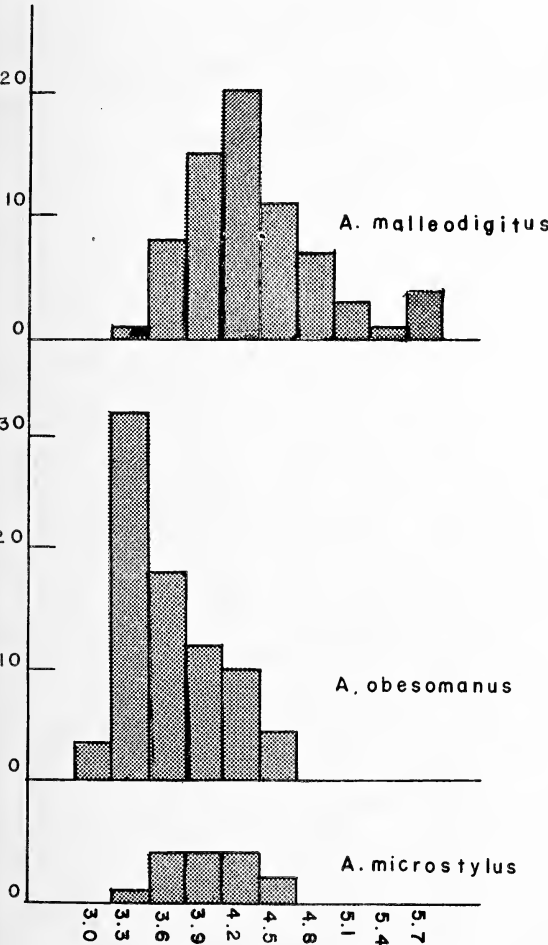


FIG. 17. *Obesomanus* group; proportions of the merus of the third leg in three species. Ordinate: the length of the merus of the third leg divided by the breadth. Abcissa: number of specimens.

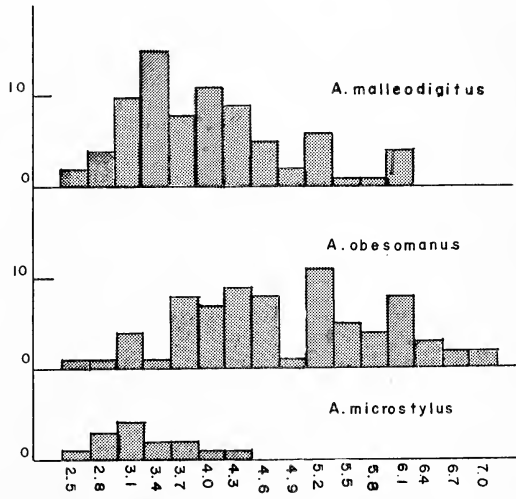


FIG. 18. *Obesomanus* group; proportions of the telson in three species. Ordinate: the length of the telson divided by the breadth of the posterior portion. Abcissa: number of specimens.

times as long as broad, instead of 7–10 times as long as broad (as taken from Bate's figures), and a more narrow posterior margin of the telson, with the telson in the variety 6 times as long as broad, instead of 3–4 times. Not enough specimens of *A. microstylus* were available to ascertain the full extent of variation on the carpus of the second legs, but in those available the length divided by the breadth of the second article varied from 6 to 8, and the telson, as illustrated by the wide span in the related *A. obesomanus*, must also be extremely variable. Therefore, this variety does not appear to be distinct, and the name should be listed in synonymy.

5. *A. lutini* Coutière. This species was characterized by having the second antennular article 1.5–2.0 times the length of the first, and 2.4–3.0 times as long as broad; the scaphocerite and carpocerite being equal, and slightly shorter than the antennular peduncle, but with the squamous portion of the scaphocerite reaching only to the middle of the second article; the grooves of the large chela being deep and pronounced, the palm of the small chela 1.5 times the length of the fingers; the second carpal article of the second legs between 2.5 and 3.5 times as long as the first; the configuration of the third legs like that of *A. obesomanus*; and the telson 6 times as long as the posterior margin is broad. As discussed above, this form is the more common type of the variable *A. obesomanus*.

6. *A. species 2*, Banner. This sole specimen from Saipan has the antennular peduncle about the same as that described for *A. lutini*, but while the carpocerite reaches to the end of the antennular peduncle, the scaphocerite reaches only to the end of the second antennular article; the palm of the second leg is twice the length of the fingers; the second and third legs are very much like those of *A. obesomanus*, and the telson is 4.1 times as long as broad. (Note: the description [Banner, 1956:352] is in error on this point; it is 4.1 times as long as the posterior margin is wide and anteriorly 2.7 times as broad as posteriorly.)

Almost all of the specimens of *A. obesomanus*

in the collection have the carpocerite and scaphocerite equal in length; however, in a few they differ in length, with the scaphocerite being shorter. Intergrading series were found in different collections that bridged the difference between a usual *A. obesomanus* and the characters noted for this species. In this provisional species, however, the orbital hoods were confluent, without a trace of rostrum, rostral keel, or orbitorostral grooves. In *A. obesomanus* there is usually a short rostrum with a short keel that is separated from the orbital hoods by a shallow concave region, but this characteristic is not constant, and in a few the rostrum is almost entirely lacking, the carina has disappeared, and the orbital hoods are almost confluent. Our present interpretation, therefore, because of the condition on the Saipan specimen, is that it merely shows an unusual variation or possibly a congenital defect.

B. Those with simple dactyli on the posterior legs, but with the second carpal article of the second leg not more than twice the length of the first.

1. *A. malleodigitus* (Bate). This species has been described twice, the original description by Bate on the basis of a fragmentary specimen, and a later redescription by de Man on a complete but smaller specimen. Unfortunately, the descriptions do not agree, and in the following synopsis the changes by de Man are put in parentheses: First antennular article equal to the sum of the following (second article 2–3 times length of visible portion of the first); spine of scaphocerite described as reaching to the end of the first antennular article, and shown as reaching to the middle of the third article (reaching from near the middle to the end of the second antennular article); squamous portion of scaphocerite narrow, tapering, two-thirds length of lateral spine (squamous portion not tapering into spine); carpocerite twice as long as scaphocerite, reaching beyond end of antennular peduncle (reaching from end of second antennular article to middle of third); fingers of small chela "about half" the length of the palm according to the description, but measuring

0.65 in the figure (a little shorter than the palm); first two carpal articles described as "subequal" and shown to have the second article about 1.5 times the length of the first (the second article varying from 1.1 to 1.6 times the length of the first); walking legs lacking from type (but described by de Man to be like those of *A. obesomanus*); telson shown to be about 3 times as long as the posterior margin is wide (4 times as long). De Man accounted for the difference by saying that his specimens were smaller and were not broken. Moreover, Bate's descriptions and figures were inaccurate.

We believe that inasmuch as Bate's type specimen was defective, as his descriptions were inadequate and did not match his drawings, and as de Man's excellent figures and descriptions agree with those of Bate on many points, the characteristics of this species should be established on the basis of the redescription by de Man. In any case, the species is well separated from those placed in Group I above by the length of the scaphocerite and by the length relationship of the first and second carpal articles of the second leg. The name *A. malleodigitus* is the oldest name in Group B.

2. *A. malleodigitus* var. *gracilicarpus* de Man. This variety was separated by de Man solely on the basis of the length: breadth relationship of the articles of the second and third legs, as given in Table 3, using figures for both the parent species and the variety as given by de Man (1911:348).

The only appendages upon which length: breadth relations were taken in our study were the second antennular article and the merus and carpus of the third legs. These show that length: breadth ratios are very variable. The graph on the merus of *A. malleodigitus* (Fig. 17) shows what might have developed into a bimodal curve, had hundreds of specimens been measured, but there is no reason to believe that those with the more slender appendages would have shown a valid specific separation from those with the heavier. Therefore we consider this variety to be merely an extreme found in a normal population.

TABLE 3
LENGTH: BREADTH RATIO OF ARTICLES

ARTICLE	<i>A. malleodigitus</i>	<i>A. m. gracilicarpus</i>
Second leg,		
fourth carpal article	2.4-3.9	5.0-5.3
Third leg,		
merus	3.7-4.0	4.5
carpus	4.4-4.8	5.6

3. *A. phrygianus* Coutière. This species was characterized by having the second antennular article 3 times the length of the first, about 4 times as long as broad; the carpocerite reaching to the end of the second antennular article; the scaphocerite to the middle of the same article, with the squamous portion only one-third the length of this article; the sculpturing of the large chela slight; the palm of the small chela about 1.2 times the length of the fingers; the second carpal article of the second legs varying from 1.1 to 1.6 times the length of the first; the length of the merus of the third leg 4 times its breadth, and feebly armed; and the telson 4.5 times as long as broad.

The actual differences between this species and *A. malleodigitus* lie in the slight differences in proportions of the appendages, which are now shown to be variable; therefore, *A. phrygianus* must be considered a synonym of *A. malleodigitus*.

4. *A. persicus* Nobili. In this species the second antennular article was described as being 3 times as long as the first, 3 times as long as broad; the carpocerite reaching almost to the end of the third antennular article; the scaphocerite reaching to the end of the second antennular article, with the squamous portion to the middle of the same article; the chelae "concerdent avec celles de phrygianus"; the second carpal article of the second legs being 1.1 times as long as the first (obviously there is a typographical error in Nobili's paper [1906:34], as it reads "1.31" instead of 1.13); the third legs being similar to those of *A.*

phyrgianus; and the telson being more than 3 times as long as broad.

Nobili distinguished his species from *A. phyrgianus* in that the second antennular article was shorter and the scaphocerite was longer; however, both of these characteristics are variable, and the proportions stated for *A. persicus* fall within the range of *A. malleodigitus*. Therefore *A. persicus*, also, should be considered a synonym.

5. *A. danae*. The characteristics set forth by Coutière are: second antennular article 2.5 times the length of first, and 4.2 times as long as broad; scaphocerite and carpocerite equal in length, reaching to the middle of the second antennular article, with the squamous portion of the scaphocerite reaching only a quarter the length of that article; the large chela lost; the palm of the small chela 2 times the length of the fingers; the second carpal article of the second leg 1.3–1.5 times the length of the first; the third leg almost identical to that of *A. phyrgianus*; the telson slightly broader than in *A. phyrgianus*, about 3.7 times as long as broad.

This species, too, is very close to *A. malleodigitus* but may be separated by the very short carpocerites; none of the specimens measured in our study approached the condition described for *A. danae*. It may be that this is merely an extreme variation, but at present this is not indicated.

6. *A. samoa* (described below). As stated below, this species is unique within the Obesomanus group in that the scaphocerite is almost vestigial, not reaching to the end of the first antennular article; otherwise the species also approaches *A. malleodigitus*.

7. *A. nobili* (nom. nov.) = *A. species* Nobili. The few characteristics given by Nobili for this specimen were: antennular and antennal peduncles like those of *A. microstylus* (therefore with the scaphocerite and carpocerite reaching beyond end of the antennular peduncle), but with the squamous portion of the scaphocerite reaching only to end of the second antennular article; the ratio of the first two carpal articles were 10:14 to 10:13; and

the carpus of the third legs a little longer than the propodus.

The combination of the characteristics of the antennal peduncles and second legs is unlike any other species in the group and, if the description is accurate, the specimen probably represents a new species; at least, it does not appear to be a variety of *A. microstylus* as Nobili suggested. We have assigned the name *A. nobili* to the tentative species.

C. Species with biunguiculate dactyli on posterior legs.

1. *A. perplexus* Banner. This species is unique within the Obesomanus group in having, in addition to the biunguiculate dactylus, crests and depressions on the large chela that are similar to those of the Megacheles group; otherwise it is similar to *A. obesomanus* and *A. malleodigitus*.

2. *A. species*, de Man. This is probably the same as *A. perplexus* (see Banner, 1956: 349).

3. *A. chamorro* Banner. This species, too, has a biunguiculate dactylus, but in general approaches the species of the Crinitus group in most characteristics, although the large chela still retains a diminished hammer-shaped dactylus.

II. Species without strong transverse articulations on the outer uropods.

1. *A. rathbunae* (Schmitt). This Caribbean species can be characterized within this subgroup by the complete absence of a rostrum and the extreme elongation of the second antennular article, as well as the narrow tip of the telson. The dactylus of the large chela does not have a strong superior (or proximal) projection.

2. *A. idiocheles* Coutière. This species has a rostrum. The scaphocerite reaches to about the middle of the second article; large and small chelae are elongate, with dactylus of the large chela formed like a single-headed, not double-headed, hammer.

3. *A. baculifer* Coutière. This species, previously known only by a female specimen, will

be shown in a later paper to be merely a female of *A. idiocheles*.

4. *A. microscaphis* (Banner). This species can be easily characterized by the extreme reduction of the scaphocerite, reaching only to or slightly past the end of the first antennular article, and by the dactylus of the large chela, which has the form of a two-headed hammer.

In summation, the following species have been retained:

A. obesomanus Dana. Synonyms: *A. lutini* Coutière, *A. species 2* Banner
A. microstylus (Bate). Synonym: *A. microstylus* var. ? de Man
A. malleodigitus (Bate). Synonyms: *A. malleodigitus* var. *gracilicarpus* de Man, *A. phrygianus* Coutière, *A. persicus* Nobili
A. danae Coutière
A. samoa (sp. nov.)
A. nobili nom. nov. Synonym: *A. species Nobili*

KEY TO THE SPECIES OF THE OBESOMANUS GROUP

1. Outer uropod with articulation	2
Outer uropod without articulation	9
2(1). Dactylus of third legs simple	3
Dactylus of the third legs biunguiculate.....	8
3(2). Second carpal article of second legs more than twice as long as first	4
Second carpal article less than twice as long as first, usually less than 1.5 times as long	5
4(3). Squamous portion of scaphocerite reaching only to middle of second antennular article	<i>A. obesomanus</i> Dana
Squamous portion of scaphocerite reaching to near end of third antennular article.....	<i>A. microstylus</i> (Bate)
5(3). Scaphocerite and carpocerite reaching to near end of third antennular article.....	<i>A. nobili</i> nom. nov.
Scaphocerite reduced, with tip reaching only to middle of second antennular article or less; carpocerite various but usually reduced	6
6(5). Scaphocerite reaching to near middle of second antennular article	7
Scaphocerite not reaching to end of first antennular article	<i>A. samoa</i> sp. nov.
7(6). Carpocerite markedly longer than scaphocerite, reaching at least to end of second antennular article	<i>A. malleodigitus</i> (Bate)
Carpocerite subequal to scaphocerite, reaching only to middle of second antennular article	<i>A. danae</i> Coutière
8(2). Large chela with crests and grooves, like those found in Megacheles group; without rostrum	<i>A. perplexus</i> Banner
Large chela smooth, without crests and grooves; with rostrum	<i>A. chamorro</i> Banner
9(1). Without rostrum (Caribbean species).....	<i>A. rathbunae</i> Schmitt
With rostrum	10
10(9). Scaphocerite reaching to middle of second antennular article; dactylus of large chela without superior projection.....	<i>A. idiocheles</i> Coutière
Scaphocerite reaching only to near end of first antennular article; dactylus of large chela with characteristic double-headed hammer shape of Obesomanus group	<i>A. microscaphis</i> (Banner)

- A. perplexus* Banner
A. chamorro Banner
A. rathbunae (Schmitt)
A. idiocheilus Coutière. Synonym: *A. baculifer* Coutière
A. microscaphis (Banner)

Alpheus obesomanus Dana

Fig. 8

Alpheus obesomanus Dana, 1852a, Acad. Nat. Sci. Philadelphia, Proc. 12:21; 1852b, U. S. Explor. Exped. Crust. 13:547, pl. 34, fig. 7. —Boone, 1935. Vanderbilt Mar. Mus., Bull. 6:135, pl. 35.

Alpheus lutini Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):885, pl. 76, fig. 24.

Alpheus species 2 Banner, 1956. Pacific Sci. 10(3):351, fig. 15.

LOCALITIES: Fiji: 2 specimens from BF 3; 1, BF 4; 6, BF 11; 1, BF 13; 2, BF 14; 5, BF 15; 3, BF 21. Tonga: 4 specimens from BT 4; 1, BT 11; 9, BT 12; 1, BT 13. Samoa: 12 specimens from BAS 1; 2, BAS 2; 4, BAS 3; 9, BAS 5; 25, BAS 6; 23, BAS 7; 9, BAS 8; 3, BAS 9; 24, BAS 10; 12, BAS 12; 12, BAS 13; 18, BAS 14; 5, BBS 1; 54, BBS 2; 4, BBS 3; 7, BBS 4; 2, BBS 7; 6, BBS 8; 20, BBS 9; 2, BBS 11; 1, BP 1; 22, BP 4; 1, BP 6; 5, BP 8; 4, BP 10; 15, BP 11; 2, BP 12; 2, BP 13; 69, BP 14.

DISCUSSION: One specimen from Samoa is noteworthy. While normal in all other respects, it is entirely lacking in antennular flagella, carpocerites, and more proximal articles of the antennal flagellar base, and the scaphocerite is degenerate, somewhat similar to that of *A. malleodigitus*. The other specimens from the same locality are normal. This has been interpreted as a possible congenital defect.

Alpheus microstylus (Bate)

Fig. 8

Betaeus microstylus Bate, 1888. Challenger Repts. 24:566, pl. 101, fig. 6.

Alpheus obesomanus de Man, 1888b. Arch. Naturg. 53:520; 1902. Senckenb. Naturf. Gesells., Abhandl. 25:867.

Alpheus malleodigitus Coutière, 1899. Les

Alpheidae, p. 223, 316, figs. 270–272, 400. [nec: *A. malleodigitus* (Bate).]

Alpheus microstylus Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):884, pl. 76, fig. 23.

LOCALITIES: Samoa: 1 specimen from BAS 10; 1, BBS 10; 1, BP 13.

Alpheus malleodigitus (Bate)

Fig. 8

Betaeus malleodigitus Bate, 1888. Challenger Repts. 24: 565, pl. 101, fig. 5.

Alpheus malleodigitus de Man, 1902. Senckenb. Naturf. Gesells., Abhandl. 25: 866.

Alpheus malleodigitus var. *gracilicarpus* de Man, 1909. V. Ned. Dierk. Ver., Tijdschr. 11(2):99.

Alpheus phrygianus Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4): 886, pl. 77, fig. 25.

Alpheus persicus Nobili, 1906. Bull. Sci. France et Belgique 40: 33.

LOCALITIES: Fiji: 1 specimen from BF 4; 4, BF 6; 1, BF 8; 2, BF 11; 2, BF 12; 4, BF 13; 1, BF 20. Tonga: 1 specimen from BT 9; 1, BT 10; 3, BT 11; 1, BT 12; 38, BT 13; 1, BT 16. Samoa: 3 specimens from BAS 5; 6, BAS 6; 9, BAS 7; 3, BAS 12; 2, BAS 13; 5, BAS 14; 1, BBS 2; 4, BBS 4; 2, BBS 5; 2, BBS 7; 20, BP 4; 6, BP 12.

DISCUSSION: For a discussion of this species see page 170.

Alpheus samoa sp. nov.

TYPE SPECIMEN: A male, carapace length 3.5 mm, collected at BAS 5. Paratype, a second male, carapace length 3.0 mm, collected at BAS 14. (Specimens and drawings lost.)

DESCRIPTION: Orbital hoods rounded, with second antennular article 5 times as long as broad, over 3.5 times as long as first and 2.7 times as long as third. Upper antennular flagellum broad, 1.2 times as long as peduncle, 1.3 mm long, without any subterminal bifurcation, lower or inner flagellum 2.2 mm long. Stylocerite reaching scarcely beyond margin of carapace, rounded. Basicerite unarmed; scapho-

cerite degenerate, triangular, acute, with tip reaching only slightly beyond end of first antennular article; carpocerite reaching to past middle (in type) or to near end (in paratype) of second antennular article; flagellum about 6 mm long. (In both specimens the antennal peduncle and most of the scaphocerite are carried under the antennular peduncle, and so they are not fully visible in dorsal view.)

Large cheliped lost in both specimens; small cheliped present only on type. Merus unarmed, slender, 4.3 times as long as broad; carpus slender; chela 5.0 times as long as broad, slightly curved; fingers slender, tapering to acute tips, 0.4 as long as chela; setae on appendage short and scattered.

Second legs asymmetrically developed, with merus of the right only 2.4 mm long, that of the left 4.0 mm long (0.5 mm longer than carapace). Carpal articles of left leg with ratio: 10:12.5:4.5:5.0:6.5; of right leg: 10:14.8:4.3:5.0:6.7; on the remaining one leg of the paratype (evidently the longer leg): 10:17.2:4.4:6.4:6.8. Ischium strongly curved (almost broken on larger leg), merus with slight proximal curving.

Third leg with ischium unarmed; merus 3.9 times as long as broad, armed on distal inferior margin with acute tooth; carpus and propodus so rotated that dactylus lies at 90° to plane of merus, similar to *A. malleodigitus*, carpus with marked twist immediately beyond meral-carpal articulation; carpus about 0.6 as long as merus, armed on distal superior and inferior margins with acute teeth; propodus slender, tapering, slightly shorter than carpus and bearing five movable spines on inferior margin, two distally; dactylus curved and simple. Fourth legs similar except meral tooth of lesser development. Fifth legs with well developed brush on propodus.

Telson 4.7 times as long as distal margin is broad, 2.5 times as broad anteriorly as posteriorly, lateral margins slightly convex, tip shallowly arcuate; medial pair of terminal spines almost as long as posterior margin is broad; dorsal spinules of moderate development. Telson without anal tubercles. Outer uropod with definite articulation.

DISCUSSION: Unfortunately, the large chela is not present on either specimen; however, we believe it would be safe to predict that the chela will be similar to those of the *Obesomanus* group or similar to those species previously placed in the genus *Thunor*. The species plainly belongs to the *Obesomanus* group. Within the group it is closest to the species previously placed in *Thunor*, which also have vestigial scaphocerites, but it may be distinguished from them by the presence of the tooth on the merus of the third legs, the form of the telson, and the presence of an articulation on the outer uropods.

The characteristics of this species demand a reconsideration of the separation of Armstrong's genus *Thunor* from the genus *Alpheus*. In a previous paper (Banner, 1956:365) the criteria for the genus *Thunor* were reviewed, and the conclusion was reached that two characteristics only would serve to separate the two genera: the lack of anal tubercles and the lack of an articulation on the outer uropod, both found in the genus *Thunor*. This species has the articulation but lacks the anal tubercles; therefore, the only criterion remaining is the articulation of the uropod. On the other hand, the species in the *Obesomanus* group and in *Thunor* present a somewhat uniform transition in other characteristics between a typical *Alpheus*-form as found in other groups, and the extreme of *Thunor*, such as *T. microscaphis* Banner or *T. rathbunae* (Schmitt). We do not believe that this single criterion is sufficient to separate *Thunor* from *Alpheus*; thus the name *Thunor* should be put into synonymy. *Thunor* could be retained, if desired, as an infrageneric group, but here again the group would be difficult to define. Therefore we are placing the species previously attributed to *Thunor* into the *Obesomanus* group, including *A. idiocheles* Coutière, in spite of the fact that Coutière placed it in the *Macrochirus* group.

CRINITUS GROUP

Alpheus frontalis H. Milne-Edwards

Alpheus frontalis Milne-Edwards, 1837. Hist. Nat. Crust. 2:356.

LOCALITIES: Fiji: 1 specimen from BF 2; 3, BF 13; 5, BF 17. Samoa: 2 specimens from BAS 1; 4, BAS 4; 12, BAS 14; 1, BBS 7; 1, BP 1; 1, BP 6a.

DISCUSSION: The Samoan specimens came from tubes of felted blue-green alga, *Lyngbya majuscula*, collected at 1–3 ft below low tide level, behind the surf zone but where the wave action was strong, at "Lions Head" on the coast east of Pago Pago Harbor (stations BAS 5, 13, 14 and BP 1).

Alpheus pachychirus Stimpson

Alpheus pachychirus Stimpson, 1860. Acad. Nat. Sci. Philadelphia, Proc. 12:30.

LOCALITIES: Fiji: 3 specimens from BF 13; 3, BF 17. Tonga: 2 specimens from BT 15. Samoa: 1 specimen from BAS 1; 5, BAS 5; 4, BAS 10; 1, BAS 13; 9, BAS 14.

Alpheus alcyone de Man

Alpheus alcyone de Man, 1902. Senckenb. Naturf. Gesell., Abhandl. 25:870, Taf. 27, fig. 61.

Alpheus aculeipes Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):892, pl. 79, fig. 31.

LOCALITIES: Fiji: 3 specimens from BF 2; 6, BF 4; 1, BF 8; 3, BF 9; 20, BF 11; 8, BF 13; 6, BF 16; 5, BF 17; 3, BF 20; 2, BF 20. Tonga: 1 specimen from BT 5. Samoa: 4 specimens from BAS 1; 1, BAS 2; 2, BAS 3; 4, BAS 6; 2, BAS 7; 22, BAS 10; 3, BAS 11; 3, BAS 12; 1, BAS 14; 11, BBS 1; 5, BBS 2; 1, BBS 3; 9, BBS 4; 2, BBS 8; 13, BBS 10; 1, BP 1; 1, BP 6; 9, BP 8; 1, BP 13; 4, BP 14.

DISCUSSION: These specimens agree very well with the descriptions of de Man and Coutière (the latter using the name *A. aculeipes*), with a single exception. Both authors state that the dactylus of the third leg bears a small but definite accessory hook; in most of these specimens a similar hook was found, but showing considerable variation in size; however, in several specimens, including two from Fiji, the accessory hook was reduced to a very slight shoulder on the inferior surface of the dactylus, a projection so slight that it

was difficult to see. A similar variation was noted by Coutière for *A. spongiorum* Coutière.

Alpheus ovaliceps Coutière

Alpheus ovaliceps Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):888, pl. 77, fig. 27.

LOCALITIES: Tonga: 5 specimens from BT 10; 20, BT 17. Samoa: 5 specimens from BAS 5; 1, BAS 10.

Alpheus bucephalus Coutière

For full citation see Banner (1957:201).

LOCALITIES: Fiji: 1 specimen from BF 13; 1, BF 16; 1, BF 17; 1, BF 18. Tonga: 1 specimen from BT 4; 4, BT 5; 2, BT 10; 10, BT 11; 5, BT 12; 1, BT 16. Samoa: 1 specimen from BAS 5; 4, BAS 6; 1, BAS 7; 1, BAS 8; 2, BAS 9; 2, BBS 2; 1, BBS 10.

Alpheus bradypus Coutière

Alpheus bradypus Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):891, pl. 78, 79, fig. 30.—Banner, 1956. Pacific Sci. 10(3):355, fig. 17.

LOCALITIES: Tonga: 27 specimens from BT 10. Samoa: 4 specimens from BAS 4; 4, BAS 7; 4, BAS 12; 2, BBS 11.

DISCUSSION: In this group of specimens some further variations were noted. The differences between the specimens from Saipan and those described by Coutière were discussed in Banner's 1956 paper. Most of the differences can be accounted for by the variation noted in this collection. For example, in 10 specimens with the small chela intact, 5 had a slightly broadened dactylus with a fringe of hairs, as described by Coutière, and 5 had the more slender and unadorned chela as described from Saipan. Further variation was noted in the length of the squamous portion of the scaphocerite, with the tip in a few reaching almost to the end of the second antennular article, and others variously between this maximum and a minimum length of less than half the length of the article; a few were asymmetrical in the development of the scale. As is common in this

group, there were variations in the relative lengths of the articles of the carpus of the second legs, in the rostral front, and in other characteristics.

Alpheus brevipes Stimpson

Alpheus brevipes Stimpson, 1860. Acad. Nat. Sci. Philadelphia, Proc. 12:30.

Crangon brevipes Banner, 1953. Pacific Sci. 7(1):103, figs. 35–37. [Neotype established.]

? *A. species* Banner, 1958. Pacific Sci. 12(2):167.

LOCALITIES: Tonga: 2 specimens from BT 2; 1, BT 9; 4, BT 10; 2, BT 11; 2, BT 13; 1, BT 17. Samoa: 1 specimen from BAS 9; 1, BP 4.

DISCUSSION: This species has previously been reported to be quite variable, both from Hawaii (Banner, 1953:103) and from other localities in the Pacific (Banner, 1956:354). Most of the specimens from these islands and other areas represented in the collection fall within the established limits of variation; however, four specimens are remarkably different.

One of the specimens is from BAS 9. The specimen is defective with most of the appendages gone. However, in all parts remaining, except for the chela, the characteristics are those of *A. brevipes*; the large chela is similar in general form, but has a more hammer-shaped dactylus, a shorter fixed finger, and has the palmar adhesive plaque set at a slight angle, and has a definite rounded transverse depression behind the adhesive plaque.

The three other specimens came from other areas. Two have been already reported from Onotoa, Gilbert Islands, as *A. species* in the *Obesomanus* group (Banner, 1958:167). The third specimen (carapace length 3.4 mm) came from collections of the Bernice P. Bishop Museum from Palmyra Island (data not available); it has not been reported before. The two Gilbertese specimens are incomplete; the Palmyra specimen is intact. The three specimens are quite constant among themselves and, with the specimen from Samoa, would be placed in *A. brevipes* without question if it were not for the form of the chela. The one

intact small chela, from the Palmyra specimen, also is similar to that of *A. brevipes*; however, the large chela is unlike any chela in the *Crinitus* subgroup, and has the appearance of an *Obesomanus*-type chela. The palm is sub-cylindrical and tapering toward the finger; the fixed finger is short and distally curved abruptly towards the appositional face; the dactylus is definitely hammer-shaped, closing beyond and over the fixed finger, and flexed far back on the face of the palm where the adhesive plaque is set low and at an angle.

None of the other specimens in the collection show variations approaching the conditions found either in these chelae or in the chela of the specimen from Samoa; therefore, it appears unlikely that these are of the same species as the common *A. brevipes* with its massive cylindrical chela. However, as *A. brevipes* is such a variable species, and because these specimens are so few, so incomplete, and from such widely different areas, and especially because they could not be distinguished from *A. brevipes* were the chelae missing, they have been retained in this species until a more adequate series can be studied.

Alpheus claudi Banner

Fig. 19

Alpheus claudi Banner, 1956. Pacific Sci. 10(3):352, fig. 16.

LOCALITIES: Fiji: 2 specimens from BF 13; 2, BF 18.

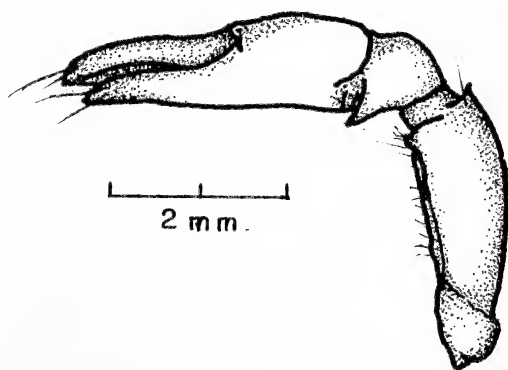


FIG. 19. *Alpheus claudi* Banner. Small chela, outer face from a 5.5 mm (carapace length) female from station BF 18.

DISCUSSION: *Alpheus claudi* was described on the basis of a single ovigerous female from Saipan, lacking the small chela. The four specimens above appear to belong to this species. Also incorporated in this discussion are two specimens from Ifaluk in the Caroline Islands. All six specimens were paired, male and female; the pairs from Fiji are rather badly broken.

First, in the shape of the rostral front, the specimen from Saipan had the anterior margin of the carapace proceeding in a gradual concave curve from the front of the orbital hoods to the tip of the undemarked rostrum; in the male from Ifaluk the shape is almost the same except that the area starts in front of the orbital hoods as a slight flattened projection. The female from Ifaluk has a marked projection before the orbital hoods, but the frontal margin is almost straight, instead of projecting further, and the very slight rostrum is demarked from this straight area. The specimens from Fiji strike a compromise between the two. All specimens have similar orbital hoods and a similar, rather marked, dorsal carinae before and between the eyes.

In two specimens from Fiji the second antennular article is more elongate, 3.5 times as long as broad, instead of 2.5 times in the other specimens from Fiji and Ifaluk; moreover, in one male from Fiji, the tip of the scaphocerite reaches only slightly beyond the end of the second antennular article, but the matching female is like the other specimens.

In the Ifaluk specimens there appears to be a strong sexual dimorphism in the large chela, with that of the female similar to the female from Saipan, but in the male of almost the same body length the chela is about 1.5 times the length and twice the thickness of that of the female, with the merus correspondingly more heavy. In one pair of specimens from Fiji there is not over 10% difference in size between the male and the female, with the male chela more like the female chela from Ifaluk and Saipan; in the other pair only the female bears large and small chelae.

The small chela was lost in the Saipan specimen; in the five specimens where it is

present it shows no sexual dimorphism except a slight difference in the relative size found in those of the Ifaluk specimens. In all specimens the fingers are about equal in length to the palm or slightly shorter, the movable finger is strongly curved, the fixed finger is flattened except on the upper edge where there is a sharp cutting ridge; on the lower margins of both fingers is a fringe of short, stiff bristles. The proximal portion of the palm has a slight but well defined shoulder. The distal portion of the inferior internal margin of the merus is either unarmed or bears a slight projection.

The second and third legs are basically similar, but in the male from Fiji again the legs are relatively thinner. Both specimens from Ifaluk have a small accessory tooth on the dactylus similar to that found in the type specimen, but none of the Fijian specimens have more than a slight rounded protuberance where the tooth would be expected.

Possibly, when additional specimens are found and examined, the specimen showing the characteristics of those from Fiji may be considered to be a separate subspecies, with slightly different rostral fronts and the lack of secondary unguis on the third legs; however, for the present it seems wiser to leave these obviously related forms in the same species and without subspecific separation.

Alpheus paralcione Coutière

Alpheus paralcione Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):895, pl. 80, 81, fig. 34.

Crangon paralcione Banner, 1953. Pacific Sci. 7(1): 99, fig. 34.

LOCALITIES: Fiji: 2 specimens from BF 17. Samoa: 1 specimen from BBS 7.

Alpheus clypeatus Coutière

Alpheus clypeatus Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):897, pls. 81, 82, fig. 36.

LOCALITIES: Samoa: 1 specimen from BAS 13; 6, BP 1; 2, BP 6.

DIADEMA GROUP

Alpheus gracilipes Stimpson

Alpheus gracilipes Stimpson, 1860. Acad. Nat. Sci. Philadelphia, Proc. 12:31.

LOCALITIES: Fiji: 14 specimens from BF 5; 14, BF 7; 22, BF 9; 1, BF 10; 5, BF 11; 2, BF 12; 32, BF 13; 10, BF 14; 2, BF 16; 12, BF 17; 3, BF 18; 15, BF 20. Tonga: 9, BT 12; 2, BT 13; 2, BT 14; 2, BT 15; 1, BT 16. Samoa: 8 specimens from BAS 8; 3, BAS 4; 2, BAS 5; 6, BAS 6; 1, BAS 8; 4, BAS 10; 5, BAS 12; 4, BAS 13; 3, BAS 14; 4, BBS 1; 4, BBS 2; 10, BBS 3; 5, BBS 5; 8, BBS 6; 3, BBS 7; 5, BBS 8; 13, BBS 9; 3, BBS 10; 1, BP 1; 4, BP 3; 1, BP 5; 7, BP 7; 2, BP 8; 6, BP 11; 4, BP 13.

Alpheus diadema Dana

For full citation see Banner, 1956.

LOCALITIES: Fiji: 1 specimen from BF 3; 2, BF 12; 2, BF 13; 2, BF 14; 2, BF 20. Tonga: 27 specimens from BT 11; 4, BT 12. Samoa: 3 specimens from BAS 1; 1, BAS 2; 1, BAS 8; 16, BAS 10; 4, BAS 12; 2, BAS 13; 5, BBS 10; 2, BP 4; 1, BP 12.

Alpheus ehlersi de Man

Alpheus ehlersi de Man, 1909a. Zool. Soc. London, Proc. 1909:663, pl. 70.

LOCALITIES: Tonga: 5 specimens from BT 5. Samoa: 5 specimens from BAS 10; 10, BBS 2; 11, BBS 3; 1, BBS 10.

DISCUSSION: These specimens agree very well with the original descriptions of de Man. The specimens show some variation, notably in the length of the stylocerite, the tip of which may reach to anywhere in the basal half of the second antennular article, in the merus of the large chela which varies from 2.2 to 2.8 times as long as broad, in the large chela itself, which varies from 2.5 to 2.8 times as long as broad, in the dactylus of the large chela which varies from rounded to a pointed tip, and in the telson, the length of which varies from 2.7 to 3.1 times the breadth of the posterior margin.

In two ways there may be slight differences between these specimens and those described by de Man. First, he describes the orbitrostral grooves as "rather deep, though narrow, grooves"; in these specimens we would prefer to call them at most moderately deep. This may be merely a matter of word usage. Second, in no specimen was the margin of the telson as convex in the basal half as shown by de Man for his specimens, although the telsons of the females are broader than those of the males; this probably is only a minor variation.

The specimens of de Man lacked their third and fourth legs; these are intact on most of the specimens available. They are sufficiently similar to the fifth leg, drawn by de Man, that further description is unnecessary, except to add that the propodus carries five spines of moderate development.

This species is surprisingly similar to *A. gracilis simplex* (Banner) of the *Macrochirus* group. When the specimens are laid side by side they may be distinguished by the differences in the orbital teeth, the orbitrostral groove, the telson, and usually by the black spine of the uropods, but the relationship of the parts of the antennular and antennal peduncles, the configuration of the thoracic appendages, including the maxillipeds and chelae, are almost the same. No intergrading specimens were found in the present collections.

Alpheus paracrinatus Miers

Alpheus paracrinatus Miers, 1881. Ann. Mag. Nat. Hist. V, 8:365, pl. 16, fig. 6.

LOCALITIES: Fiji: 4 specimens from BF 2; 14, BF 5; 6, BF 7; 3, BF 8; 12, BF 9; 3, BF 10; 3, BF 11; 17, BF 13; 3, BF 14; 18, BF 18; 3, BF 19; 5, BF 20. Tonga: 1 specimen from BT 11; 7, BT 12; 4, BT 14; 6, BT 17. Samoa: 3 specimens from BAS 1; 2, BAS 2; 3, BAS 3; 9, BAS 5; 2, BAS 7; 2, BAS 8; 2, BAS 9; 30, BAS 10; 6, BAS 12; 8, BAS 13; 9, BAS 14; 13, BBS 1; 6, BBS 2; 10, BBS 3; 7, BBS 4; 1, BBS 6; 3, BBS 8; 20, BBS 9; 2, BBS 10; 1, BP 1; 3, BP 3; 10, BP 5; 2, BP 6; 6, BP 7; 6, BP 8; 4, BP 9; 1, BP 11; 6, BP 13.

Alpheus alpheopsides Coutière

Alpheus alpheopsides Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):901, pl. 83, fig. 40.

LOCALITY: Samoa: 2 specimens from BAS 12.

BREVIROSTRIS GROUP

Alpheus rapax Fabricius

Alpheus rapax Fabricius, 1798. Suppl. Ent. Syst. p. 405.

LOCALITY: Tonga: 1 specimen from BT 14.

DISCUSSION: This sole female agrees almost perfectly with the specimens from Hawaii and with the descriptions of the species, except that the rostrum reaches to the end of the first antennular article. However, in the Hawaiian specimens the rostrum was found to vary in length and this specimen does not greatly exceed the longest in that series.

Alpheus savuensis de Man

Alpheus savuensis de Man, 1908. Leyden Mus., Notes 30:110. 1911. Siboga Exped. 39a¹(2):392, pl. 20, fig. 90.

LOCALITY: 2 specimens from BP 13.

DISCUSSION: Our specimens agree very well with de Man's, except that the stylocerite is a little longer and it does have a definite spine which reaches to the end of the first antennular article. In de Man's specimens the "acute point of stylocerite curved inward, [and was] not spiniform" (1911:392).

EDWARDSI GROUP

Alpheus coutierei de Man

Alpheus coutierei de Man, 1909b. V. Ned. Dierk. Ver., Tijdschr. 11(2):107. 1911. Siboga Exped. 39a¹(2):409, pl. 22, 23, fig. 97.

LOCALITIES: Fiji: 2 specimens from BF 19; 4, BF 20. Tonga: 1 specimen from BT 18. Samoa: 9 specimens from BBS 10.

DISCUSSION: In this species the rostrum is pronounced and triangular, broader than is

usual for this group, and reaches at least to the middle of the first antennular article. Its lateral margins are a continuation of the front of the orbital hoods, and are at most set off by an indistinct triangle. The carina is sharp but variable in length, extending in some specimens to slightly posterior to the orbital hoods and in others to the anterior cardiac region.

The ratio of the antennular articles in these 16 specimens runs from 1: 1.8: 0.9 to 1: 2.0: 1. The outer margin of the squame is sharply curved and its spine reaches to the end of the last antennular article.

The large chela is a little over 2 times as long as broad. Its merus, also more than 2 times as long as broad, has along its inferior internal margin a row of small tubercles and terminates in a small sharp preapical spine. The small chela is 3 times as long as broad, carries a row of tubercles along the inferior internal margin of the merus but lacks the terminal spine. The second legs are absent in all the specimens. The third legs, available in only three specimens, show a length-breadth ratio from 4.1 to 5.0. There is no spine on the inferior margin of the merus.

These specimens agree well with de Man's original description except for two characteristics. First are the tubercles on the inferior internal margin of the merus of the large and small chela, which de Man pictures as prominent (1911: Fig. 97 d-e), while those of our specimens are very small. Second, de Man states that the abdominal pleura are all produced into angles. In the males only the first pleura were cordiform and produced into obtuse angles, with the more posterior pleura being rounded; in the females all pleura were rounded. These differences may be of systematic importance, but without a more extensive group of specimens it is impossible to determine whether these are an individual variation or subspecific differences.

A. coutierei was separated by de Man from *A. bowvieri hululensis* Coutière on the basis of several characteristics which include length of the rostral carina. This group of specimens has shown the rostral carina to be variable in length, and *A. coutierei* appears to be the

same as *A. bouvieri hululensis*. In Banner and Banner (1964), *A. bouvieri* has been placed in synonymy under *A. leviusculus* Dana, leaving standing the "variety" Coutière attributed to *A. bouvieri* as a separate species *A. hululensis*. If *A. hululensis* and *A. coutierei* are deemed to be the same, the name *A. hululensis* will take priority.

Alpheus ladronis Banner

Alpheus ladronis Banner, 1956. Pacific Sci. 10(3):360, fig. 20.

LOCALITIES: Samoa: 1 specimen from BP 3; 1, BP 6; 1, BP 7; 37, BP 10; 2, BP 11; 3, BP 13.

Alpheus crassimanus Heller

Alpheus crassimanus Heller, 1865. Reise der Novara . . . Zool. Theil 2(8):107, pl. 10, fig. 2.—Bate, 1888. Challenger Rpts. 24: 554, pl. 99, fig. 2.—de Man, 1902. Senckenb. Naturf. Gesell., Abhandl. 25: 880, pl. 27, fig. 62.

Alpheus lobidens Coutière, 1897a. Leyden Mus., Notes 19:199.

Crangon crassimanus Banner, 1953. Pacific Sci. 7(1):134–138, fig. 49.

LOCALITIES: Fiji: 11 specimens from BF 1; 2, BF 12; 4, BF 13. Tonga: 6 specimens from BT 15. Samoa: 5 specimens from BBS 9; 2, BP 2; 3, BP 13; 8, BP 15.

Alpheus strenuus Dana

Fig. 20

Alpheus strenuus Dana, 1852a. Acad. Nat. Sci. Philadelphia, Proc. 6:21; 1852b. U. S. Explor. Exped. 13:543, pl. 34, fig. 4.—Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):913, pl. 87, fig. 53.—Pearson, 1911. Spolia Zeyland. 7(28):185, pl. 7, fig. 6.

Alpheus strenuus angulatus Coutière, 1905. Fauna and Geog. and Mald. and Laccad. 2(4):914.

LOCALITIES: Fiji: 10 specimens from BF 1; 2, BF 3; 14, BF 9; 1, BF 19. Tonga: 4 specimens from BT 8; 4, BT 11; 1, BT 12; 9, BT 14; 2, BT 17. Samoa: 1 specimen from BAS 9; 10, BAS 10; 1, BBS 2.

DESCRIPTION: Body very large, but of normal alpheid proportions, neither heavy nor slender. Rostrum slender, acute, without setae, tip reaching to just beyond end of first antennular article, arising basally from rounded ridge extending posteriorly between orbital hoods. Areas between ridge and orbital hoods in the form of a shallow rounded groove, becoming more shallow posteriorly; portions of frontal margin lying lateral to rostrum are concave. Orbital hoods of normal shape, rounded and without teeth. Profile of anterior dorsal portion of carapace sloping ventrally.

Antennular peduncles with second article 2.3 times as long as broad, 1.6 times as long as visible portion of first and 2.6 times length of third article; second article tapering slightly distally. Upper flagellum about 1.6 times as long as peduncle, with broadened basal portion over half length of flagellum; lower flagellum about 4 times length of peduncle. Stylocerite with narrowed acute tip reaching slightly past end of first antennular article.

Scaphocerite well developed, with lateral spine reaching beyond end of antennular peduncle; rounded squamous portion reaching almost to the end of same peduncle; outer margin slightly curved and concave. Basicerite with acute, slender tooth on inferior internal angle. Carpocerite reaching to level of end of antennular peduncle. Antennal flagellum long, capable of reaching behind telson.

Third maxillipeds with ultimate article 1.7 times length of penultimate; distal article armed on inner side and upper margin with dense, short, stiff setae and only scattered longer setae along margins; terminal bristles considerably shorter than last article.

Ischium of large cheliped unarmed. Merus with outer face 2.4 times as long as broad; superior apex rounded, not projecting; inferior internal angle with a large projection distally, tipped with a small, curved, acute tooth; merus otherwise unarmed. Chela 2.3 times as long as broad, with the fingers occupying 0.38 the length of the entire chela; breadth of chela at point of articulation of the fingers 0.7 that of maximum breadth of palm. Superior margin distally developed into a heavy rounded ridge

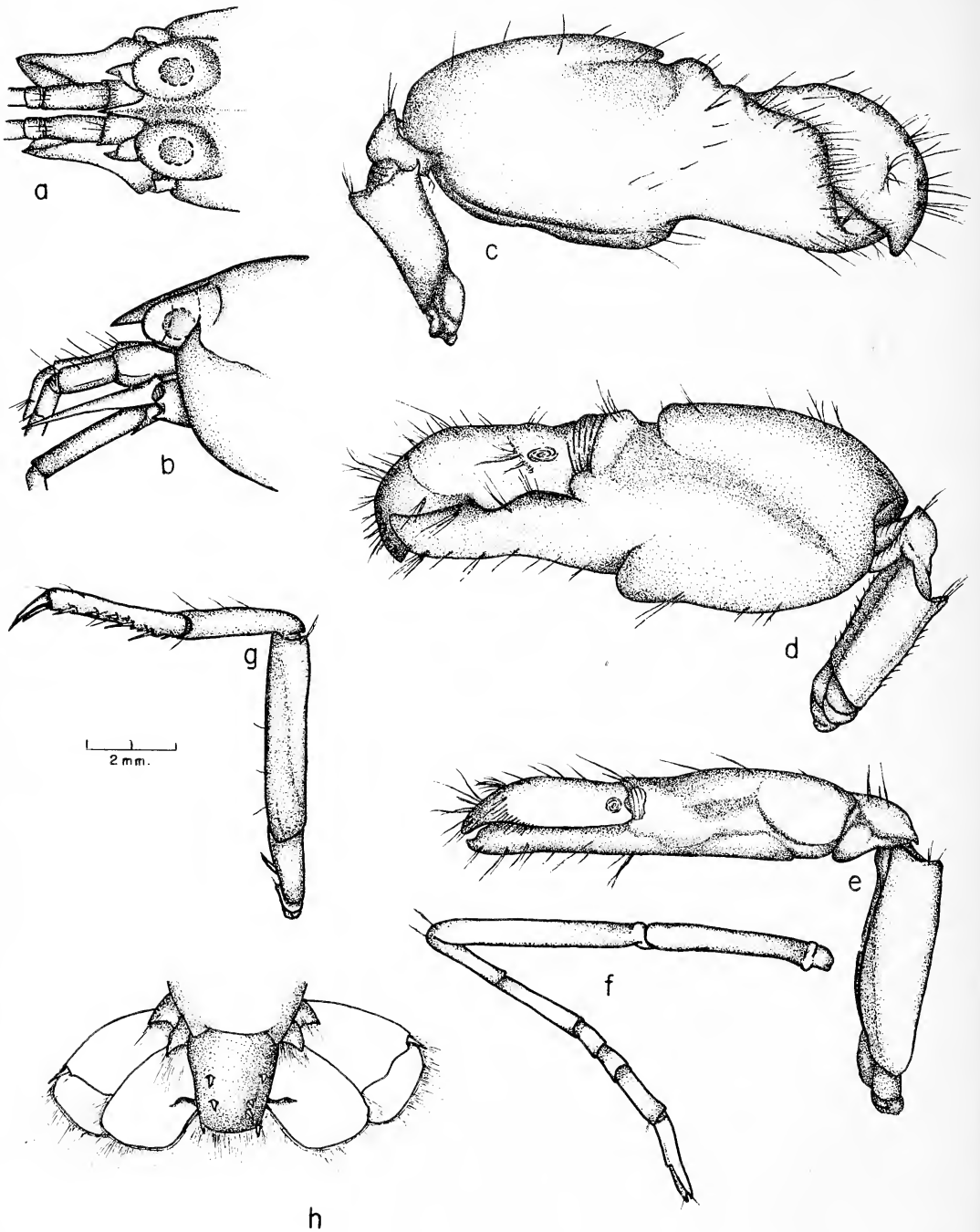


FIG. 20. *Alpheus strenuus* Dana. 10 mm (carapace length) male from BT 14. *a, b*, Anterior region, dorsal and lateral aspects; *c, d*, large cheliped, lateral and medial aspects; *e*, small cheliped, lateral aspect; *f*, second leg; *g*, third leg; *h*, telson and uropods.

that projects as a rounded lobe overhanging the transverse groove. Transverse groove continued into triangular depressed area on outer face; depressed area with margins gradual and rounded, well defined only on inferior side; proximal apex of triangular area continued as a shallow groove that follows the *linea impressa* proximally to near base of palm. Lower shoulder on outer face strong but rounded. On inner face of palm transverse groove continued into two ill-defined depressions, one running inferiorly to form depression before lower shoulder, the other continued proximally towards the middle of the palm face. Dactylus heavy, curved, with its distal portions crossing fixed finger; tip slightly longer than fixed finger. Palmar and dactylar adhesive plaques small. Scattered setae only on distal portion of chela.

Merus of smaller cheliped 2.5 times as long as broad; distal end of superior margin unarmed and rounded; inferior internal margin terminated with a small, acute tooth. Carpus with flat, subacute toothlike projection on superior margin projecting over base of propodus. Chela proper 2.2 times length of merus, 0.7 length of large chela; 3.6 times as long as broad, with the fingers occupying 0.42 the total length. Palm with slight compression, bearing shallow rounded and ill-defined depressions on superior margin and both faces, similar to those of large chela but not as extensive; without any trace of inferior shoulder as found on large chela. Fringe of bristles on dactylus well developed; tip sharp, hooked, and crossing similar tip of fixed finger; both fingers with low, sharp ridge extending along inner margin of appositional surface. Distal portion of inner face of chela with scattered long setae.

Carpal articles of second legs with ratio 10:9:3:3:6, second article 5 times as long as broad; chela subequal in length to second article.

Third legs with ischium armed with a strong movable spine; ischium 0.42 as long as merus. Merus unarmed, 4.4 times as long as broad, with slight distal taper. Carpus 0.5 length of merus, with distal angles not developed into teeth

nor bearing spines. Propodus 0.7 length of merus, tapering distally, bearing about 13 spines and spinules along inferior margin. Dactylus curved, acute, simple, 0.23 length of merus and 0.33 length of propodus, bearing several groups of short stiff setae toward tip.

Uropods of normal form, unarmed except for curved spine at shoulder of outer branch. Telson twice as broad at maximum breadth as at posterior tip; length 2.8 times breadth at tip; lateral margins slightly but regularly convex, tip broadly arcuate; lateral terminal spines slight and inconspicuous; dorsal spines well developed.

No apparent sexual dimorphism except in form of abdominal pleura of ovigerous females; large and small chelae in female identical with those of male.

DISCUSSION: *Alpheus strenuus* is a member of a series of species in the Edwardsi group that are separated by subtle differences, often based upon later interpretations of the rather inadequate descriptions and figures of the earliest workers on the family; to evaluate the validity of these species, either the type specimens should be redescribed in detail, or, where the type is lost, a neotype should be designated and described. In addition, a study of the variation within the species should be made, to see if it encompasses other nominal species.

Because Dana's type for this species has been lost, as were so many of the other species of crustaceans that he described, and as the type locality for his species was Tonga, we collected, described, and depicted a specimen as a neotype from Tonga for our original (destroyed) paper. Dana did not specify where on the island of Tongatabu he collected his specimens; our neotypic series was collected within walking distance of the usual landing place at Nuku'alofa, possibly in the exact area where Dana collected his specimens. The neotype-to-be was the largest specimen from Tonga, 37 mm long, and shorter than Dana's, which was $1\frac{3}{4}$ inches, or about 44 mm. However, specimens from other islands in our collections reached the length of 62 mm. The only difference between the specimen designated as the neotype and the description and

figures of Dana lay in the large chela, which he shows as having the terminal projection of the superior margin at right angles to, but not overhanging, the transverse groove.

Of our efforts to establish a neotype only the description above, and the notes following, remain. Most of the specimens of the neotypic series and the figures of the neotype were destroyed. Of the five specimens from Tonga saved from the fire, four were incomplete and the fifth was too much smaller than Dana's original to be designated as a neotype. This last specimen, taken from BT 14, with the carapace length of 10 mm, we have drawn and are offering to future workers as an example of a small specimen from the type locality.

Alpheus strenuus is a very widespread and common species, and was represented in our study collection by over 150 specimens. At Eniwetok in the Marshall Islands a large number were collected from a single environment so that the extent of variation could be determined. A selection of both sexes and of varying sizes, together with random samples from other archipelagoes, was carefully measured; all other specimens were examined but not measured.

In all, 20 specimens were measured. The form and size of the rostrum and orbital hoods were found to be constant. The ratio of the antennular articles varied as follows (considering the length of the first article to be unity): 1: (1.4–2.1): (0.6–1.0); the second article was from 1.5 to 2.7 times as long as broad. In the specimen described above the second article was 1.6 times the length of the first and 2.3 times as long as broad. The tip of the stylocerite in all cases reached to, and in a few cases slightly beyond, the end of the first antennular article. The relative lengths of the carpocerite and scaphocerite varied only slightly, with the two subequal and slightly longer than the antennular peduncle. The spine of the basicerite was always present and acute. On the large chela the general form remained constant, with the upper margin terminating in an obtuse tooth that overhung the transverse groove. The length of the entire chela varied from 2.0 to 2.8 times the length of the fingers. The merus of the cheliped showed

greater variation, ranging from 1.7 to 2.8 times as long as broad (2.4 in specimen described), the larger specimens in general having the broader merus. The tooth on the merus was of constant development. On the small chela all individuals, regardless of size or sex, had the *balaeniceps*-shaped dactylus; however, there was variation in the sculpturing of the palm, with some individuals showing traces of the inferior shoulder. The fingers of this chela were 0.40–0.47 the length of the entire chela. The merus of the small cheliped, like the merus of the large cheliped, was more slender in smaller specimens, ranging from 1.8 to 3.0 times as long as broad; in one specimen the tooth on the inferior internal margin was obtuse rather than acute. The carpal articles of the second legs showed only minor variation, with the range of the ratios as follows: 10: (8–11): (3–4): (3–4): (4–6). On the third leg the ischial spine was always present; the merus varied from 3.3 to 5.0 times as long as broad; the carpus was from 0.5 to 0.8 times the length of the merus, and the propodus 0.6 to 0.7 the length of the same article. The maximum breadth of the telson was from 1.8 to 2.5 times the breadth of the tip.

The smallest specimen in the collection had a carapace length of 3 mm, and was collected with the large number of large *A. strenuus* at Eniwetok; this showed the characteristics of large specimens except for minor differences in the chela. The sculpturing on the large chela was not as pronounced as in mature specimens, and the termination of the upper margin did not overhang the groove; the small chela was heavier in proportion to the length, and the sculpturing was poorly developed.

Two varieties or subspecies of this species have been described: *A. strenuus angulatus* Coutière (1905:914) and *A. strenuus galapagensis* Sivertsen (1934:3). Coutière's subspecies was based on three characteristics: first, a more slender merus of the third legs, being almost 5 times as long as broad; second, a more elongate second article of the carpus of the second legs, being 1.1 times the length of the first; and, third, an inferior margin of the merus of the third leg being "plus rectiligne . . .

et forme à l'apex antérieur un angle saillant . . ." The first two characteristics fall easily within the range of variation reported above. The third appears to be too subtle and inconstant to be reliable. Therefore we consider Coutière's subspecies to be invalid. On the other hand, the form described by Sivertsen appears to be quite distinct, especially in the form of the rostrum, which in his subspecies does not reach to the middle of the visible portion of the first antennular article. On the basis of its characteristics and its geographic isolation we regard it as a valid subspecies.

This species is separated from all other Edwardsi species, when they are of normal and usual development, by the presence of a *balaeniceps* dactylus on the small chela of both sexes. If the male only is present in a collection, or if the specimens lack intact small chelae, then separation between this and such related species as *A. crassimanus*, *A. pacificus*, *A. audouini*, etc. is indeed difficult, but distinction may usually be made by the shape of the proximal margin of the transverse groove and the inferior shoulder on the large chela. Another differentiating characteristic may be found in the setae on the last article of the third maxilliped. However, in two species of the complex some females have been reported as bearing at times setiferous crests on the dactyli of the small chela characteristic of *A. strenuus*. Coutière stated that the females of his species, *A. audouini*, did at times ("*n'est pas rare*") have traces of the crests normally found only in the males (1905:914). This species, in that case, may be distinguished from *A. strenuus* only by subtle differences in the form of the large chela, which can be seen by comparing Coutière's figures 52 and 53 (1905: Pl. 87). *A. pareuchirus* Coutière var. *imatrix* de Man (1909b:106) was separated from the parent species by the fact that the female bears *balaeniceps* chela. Those females may be distinguished easily in the form of the large chela, which is more elongate and in which the lower shoulder is indicated only by a shallow rounded depression; the third legs are also more slender and tapering.

There has been considerable doubt in our

minds, as there has been in the minds of previous workers, about the specific distinctions within this group of related species, which includes *A. strenuus*, *A. audouini*, *A. edwardsi*, *A. pacificus*, and *A. chiragricus*. All are of large size and somewhat similar form. Careful examination, however, has left us convinced that *A. strenuus* at least is a separate and valid species, and that the form of the chela in the female is an excellent specific character.

A. strenuus is of wide distribution in the Pacific, being recorded from numerous islands from the Indian Ocean to Tahiti. Most of the specimens recorded here were collected under rocks on sandy beaches in the lower portion of the intertidal zone.

Alpheus pacificus Dana

Alpheus pacificus Dana, 1852a. Acad. Nat. Sci. Philadelphia, Proc. 6:21; 1852b. U. S. Explor. Exped. 13:544, pl. 34, fig. 5.

LOCALITIES: Fiji: 5 specimens from BF 3; 1, BF 21. Samoa: 1 specimen from BP 10; 4, BP 11.

Alpheus parvirostris Dana

Alpheus parvirostris Dana, 1852a. Acad. Nat. Sci. Philadelphia, Proc. 6: 22. 1852b. U. S. Explor. Exped. 13:551, pl. 35, fig. 3.

LOCALITIES: Fiji: 4 specimens from BF 4; 3, BF 5; 2, BF 6; 7, BF 7; 6, BF 8; 1, BF 10; 5, BF 11; 3, BF 12; 3, BF 14; 3, BF 15; 2, BF 16; 1, BF 17; 1, BF 19; 11, BF 20. Tonga: 2 specimens from BT 1; 4, BT 2; 27, BT 4; 13, BT 5; 7, BT 8; 4, BT 9; 2, BT 10; 20, BT 11; 45, BT 12; 2, BT 13; 1, BT 16. Samoa: 13 specimens from BAS 1; 40, BAS 2; 3, BAS 3; 37, BAS 6; 24, BAS 7; 3, BAS 8; 16, BAS 9; 10, BAS 10; 21, BAS 11; 33, BAS 12; 54, BAS 13; 28, BAS 14; 27, BBS 1; 68, BBS 2; 23, BBS 3; 25, BBS 5; 1, BBS 2, BBS 6; 9, BBS 7; 17, BBS 8; 22, BBS 10; 2, BBS 11; 1, BP 3; 3, BP 1; 2, BP 4; 5, BP 5; 8, BP 6; 12, BP 8; 1, BP 9; 9, BP 10; 6, BP 11; 6, BP 12; 11, BP 13; 15, BP 14.

Alpheus hippothoe de Man

Alpheus hippothoe de Man, 1888a. Linn. Soc. London, Journ. 22:268, pl. 17, fig. 1-5.

LOCALITIES: Fiji: 1 specimen from BF 13; 2, BF 14. Tonga: 1 specimen from BT 1; 32, BT 7.

DISCUSSION: These specimens, according to our partially burned notes, showed some characteristics that were closer to those of *A. edamensis* de Man than of *A. hippothoe*, especially in slight differences in relative proportions of the appendages. With the loss of the specimens, the characteristics cannot be reviewed.

Alpheus funafutensis Borradaile

For full citation see Banner and Banner (1964:96).

LOCALITIES: Tonga: 2 specimens from BT 10. Samoa: 4 specimens from BP 10.

Alpheus edamensis de Man

Alpheus hippothoe var. *edamensis* de Man, 1888b. Arch. für Naturgesch. 53(1): 518. Lenz, 1905. Senckenb. Naturf. Gesell., Abhandl. 27:383.

Alpheus edamensis de Man, 1911. Siboga Exped. 39a¹(2):437, pl. 23, fig. 107.

Alpheus acanthomerus Ortmann, 1890. Zool. Jahrb. 5:474, pl. 36, fig. 12.

nec *Alpheus hippothoe* var. *edamensis* de Man, 1897. Zool. Jahrb. 9:757. 1902. Senckenb. Naturf. Gesell., Abhandl. 25: 891.

LOCALITIES: Fiji: 4 specimens from BF 5; 3, BF 13; 2, BF 15; 2, BF 17; 5, BF 18; 3, BF 20; 2, BF 21. Samoa: 2, BAS 1; 2, BAS 13; 1, BBS 3; 2, BBS 7; 4, BBS 10.

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An Interpretation of the Relationships Among the Species of *Parapercis*, Family Mugiloididae

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THIS WORK IS BASED on data taken from the descriptive study by Cantwell (1964) of the genus *Parapercis*, fishes of the Indo-Pacific oceans. The descriptions were based on anatomical studies, and each structure was analyzed to determine its variation within a species and its value in identification.

Here an effort is made to employ those characters showing the least variation within species to establish possible affinities between species, to define species groups, and to determine relationships among them.

METHODS

Using the method described by Cain and Harrison (1958), seven characters were utilized to determine the affinity of the members of this genus. The characters used were the number of teeth in the outer row of the lower jaw, dorsal spines, dorsal rays, total anal rays, caudal vertebrae, the shape of the spinous dorsal, and the connection between the spinous and soft dorsal. The latter two characters, not being measurements or meristic data, were assigned numerical values: 5 was given if the dorsal spines became progressively longer posteriorly; 4 if the middle spines were longest; 3 if the membranes were attached to the first soft dorsal ray opposite the tip of the last spine; and 2 if a connection occurred at the base of the first soft dorsal ray.

Briefly, this method obtains a combined value for the differences between two forms. An example of this method is given (Tables 1 and 2), using only 5 of the 26 species. First, the means of the measurements of the same characters in all the forms were obtained. Next, all the mean values for each character were divided by the maximum mean value for that character; this gives the reduced values and removes the

bias produced by the different units of measurement (Table 1). Third, all the forms are compared with each other, two at a time, by obtaining the differences between the reduced values of each character (Table 2). Low values imply close affinity, higher values more distant relationship.

When the species are compared with each other, two at a time (Table 2), the total differences fall into two categories. Species A, B, and C are very much alike, and are different from D and E, which resemble each other closely.

RESULTS

Comparisons of all 26 species of the genus, using this method, show the presence of six groups of species with great affinity toward each other. The mean differences of reduced values within these groups are: I, 18.8; II, 10.0; III, 3.2; IV, 21.7; V, 0.0; and VI, 6.4. In every instance each member of a group has a greater affinity for the other members of its own group than for any member of any other group. These groups are listed below.

GROUP I: *binivirgata*, *multifasciata*, *mima-seana*, *sexfasciata*, *muironis*, *aurantiaca*.

GROUP II: *cylindrica*, *haackei*, *ommatura*, *pulchella*, *snyderi*.

GROUP III: *emeryana*, *filamentosa*, *nebulosa*, *schauinslandi*, *alboguttata*.

GROUP IV: *cephalopunctata*, *tetracantha*, *xanthozona*, *hexophthalma*, *clathrata*, *polyophthalma*.

GROUP V: *ramsayi*.

GROUP VI: *colias*, *gilliesi*, *allporti*.

The mean differences of reduced values between groups give the degree of relationship among groups, as shown in Table 3.

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TABLE 1
REDUCED VALUES OF SEVEN CHARACTERS FOR FIVE SPECIES OF THE GENUS *Parapercis*

CHARACTER	SPECIES				
	A	B	C	D	E
Caudal vertebrae	99.6	99.3	100.0	90.1	90.3
Dorsal spines	98.8	97.4	98.4	98.8	98.8
Dorsal rays	94.5	94.7	95.2	90.4	86.5
Anal rays	99.0	99.4	100.0	94.1	89.3
Teeth in outer row of lower jaw	80.0	60.0	80.0	60.0	60.0
Shape of spinous dorsal	100.0	100.0	100.0	80.0	80.0
Connection from spinous dorsal	100.0	100.0	100.0	67.0	67.0

TABLE 2
DIFFERENCES BETWEEN THE REDUCED VALUES: FORMS COMPARED WITH EACH OTHER,
TWO AT A TIME

CHARACTER	SPECIES									
	A-B	A-C	A-D	A-E	B-C	B-D	B-E	C-D	C-E	D-E
Caudal vertebrae	0.3	0.4	9.5	9.3	0.7	9.2	9.0	9.9	9.7	0.2
Dorsal spines	1.4	0.4	0.0	0.0	1.0	1.4	1.4	0.4	0.4	0.0
Dorsal rays	0.2	0.7	4.1	8.0	0.5	4.3	8.2	4.8	8.7	3.9
Total anal rays	0.4	1.0	4.9	9.7	0.6	5.3	10.1	5.9	10.7	4.8
Teeth in outer row of lower jaw	20.0	0.0	20.0	20.0	20.0	0.0	0.0	20.0	20.0	0.0
Shape of spinous dorsal	0.0	0.0	20.0	20.0	0.0	20.0	20.0	20.0	20.0	0.0
Connection from spinous dorsal	0.0	0.0	33.0	33.0	0.0	33.0	33.0	33.0	33.0	0.0
Total	22.3	2.5	91.5	100.0	22.8	73.2	81.7	94.0	102.5	8.9

The analysis of these data indicate that Group VI, those species found only near the south-eastern tip of Australia, Tasmania, and New Zealand, are more closely related to those species found in Japanese waters (Group I), than to those groups in the central west Pacific and the Indian oceans. *P. ramsayi*, the only species in Group V and from southeastern Australia, is also more closely related to those forms from Japan than to those from the central west Pacific area. The only species endemic to the Hawaiian Islands, *P. schauinslandi*, was found to have a greater affinity for those species of the central west Pacific and Indian oceans than for those found primarily in Japanese waters or in southeastern Australia and New Zealand.

This close relationship between those species of Japanese and southeastern Australian waters supports the phenomenon of bipolarity. Bipolarity, or amphipolarity, is defined by Ekman (1953: Chap. 11) as bipolar taxonomic development which presupposes a center of distribution in the tropics, which served as an intermediary link between amphipolar species. Sverdrup et al. (1942:849) refer to this phenomenon as bipolarity of relationship, and define it as "a bipolar distribution in which animals of higher latitudes are more closely related taxonomically to each other than to those of lower latitudes."

Another phenomenon of parallel development exhibited by the species of the genus *Parapercis* is the larger size of the colder water forms. The mean greatest body depths of all species from Australian, Indo-central Pacific, and Japanese waters are, respectively, 195.2, 163.2, and 184.9, with mean least body depths, respectively, of 95.4, 87.8, and 94.5. The longest individuals are also taken from Australia and Japan.

DISCUSSION

The horizontal distribution of this genus is characteristic of many littoral fishes and other littoral fauna of the tropical and subtropical Indo-Pacific oceans. The great expanse of water in the East Pacific Ocean forms a barrier against dispersal of many of the shore forms to the west coast of America, whereas temperature plays an

TABLE 3
MEAN DIFFERENCES OF REDUCED VALUES
BETWEEN GROUPS OF SPECIES OF THE GENUS
Parapercis

GROUP	I	II	III	IV	V
I					
II	81.5				
III	89.2	33.6			
IV	55.9	65.7	51.0		
V	44.7	86.7	96.8	61.4	
VI	48.3	70.7	88.3	51.3	79.1

important role in restricting warm water animals from migration around the southern tip of Africa. Temperature is also the limiting factor in northern and southern latitudes for littoral animals of this large faunal area.

The genus *Parapercis* ranges from southern Japan to the Hawaiian and Tuamotu islands, southwestward to New Zealand and Tasmania, west to Durban on the east coast of Africa, thence north to the Red Sea and across the Indian Ocean.

The Indo-Malayan subregion of the Indo-west Pacific contains 11 of the 26 species of the genus, *filamentosa* being the only one endemic to this area. The number of representatives decreases in a westerly direction, with only 1 species, *nebulosa*, found on the east coast of Africa as far south as Durban. The subregion consisting of the islands of the central Pacific excluding Hawaii has but 5 species, none of which is endemic to this subregion. *P. schauinslandi*, 1 of 2 species found in Hawaii, has not been reported from any other subregion. Of the 10 species of the subtropical Japanese waters, 4 are endemic to this subregion: *mimaseana*, *muronis*, *sexfasciata*, and *aurantiaca*. The Solanderian province of northeast Australia contains 5 species, while the Dampierian province in the northwest has 2, none of which is endemic. In the south the Peronian province has 6 representatives, of which *binivirgata*, *baackei*, *allporti*, and *ramsayi* are common to no other subregion. *P. colias* and *gilliesi*, the only 2 species of the genus taken from New Zealand waters, are also endemic to this area.

Using the Indo-Malayan subregion as the approximate center of the geographic range of this genus, the above distributional data indicate that the further one moves away from this center, in any direction, the more the addition of endemic species replaces the progressively depleted Indo-Malayan forms. Speciation, as the data indicate, has taken place on the periphery of the range, i.e., in those areas of comparative geographic isolation.

Mayr (1942), Darlington (1948), and Brown (1957 and 1958) agree that geographic isolation plays a major role in the process of evolving distinct species, although there is one great point of difference among the three. Darlington and Brown state that an adaptive change occurs in the center and spreads out to the periphery; then the population recedes, leaving some members isolated. Another change occurs in the center and spreads outward. If this second change is different enough from the previously isolated populations on the periphery, a new species is recognized. Mayr, however, postulates that "a new species develops if a population which has become geographically isolated from its parental species acquires, during the period of isolation, characters which promote or guarantee reproductive isolation when the external barriers break down."

The data presented here, showing the comparatively large numbers of endemic species on

the periphery of the range, support these modern views on speciation in that geographic isolation plays a major role in the formation of distinct species. The data, however, do not favor either viewpoint as to where the adaptive changes occur.

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Bilateral Asymmetry in Paired Meristic Characters of Pacific Salmon

B. J. LANDRUM¹

ABSTRACT: The presence, extent, and direction of bilateral asymmetries of lateral line scales, gill rakers, branchiostegal rays, and pectoral fin rays of sockeye, chum, and pink salmon were examined. Some asymmetries were found in all characters in each species. Asymmetries, considering all species combined, occurred in approximately 72% of the lateral line scale comparisons, 59% of the gill raker comparisons, 70% of the branchiostegal ray comparisons, and 26% of the pectoral fin ray comparisons. Bilateral variation in these characters was not conclusively related to sex of the specimens; however, some tendency toward greater asymmetry in branchiostegals of females was shown. Complete evaluation of this tendency will require further examination.

Occurrences of asymmetries were evaluated in relation to the reliability of substituting counts from the opposite side when the chosen side was lost or severely damaged. Substitution of lateral line scales of sockeye salmon appeared to be feasible, but in chum salmon the right side counts were significantly greater. (Scale counts from pink salmon were not available, because of the extreme difficulty in obtaining reliable counts of the characteristically small scales.) Gill raker counts from sockeye salmon were found not to be interchangeable, as the right side counts significantly exceeded those of the left. In pink and chum salmon, bilateral variations in gill rakers appeared to be equal. Branchiostegal counts from the left sides of all species were significantly greater than those of the right. It was indicated that, for all species, pectoral fin ray counts from either side could be substituted reliably.

BILATERAL ASYMMETRY in various body parts has been recognized in many animals that have a bilaterally symmetrical form of development. The extent and cause of many asymmetries have not been defined. Asymmetries of fish in the order Pleuronectiformes (flatfish) result in normally dextral or sinistral individuals and have been attributed generally to the processes of natural selection and adaptations of the organism to life on the ocean bottom. Hubbs and Hubbs (1944:303), emphasizing the morphology of flatfish, have pointed out that some asymmetries appear in many body parts of all fishes, both externally and internally. In studies on meristic and other characters of four species of chars, Vladykov (1954:910) has noted somewhat

higher gill raker counts on the right sides. In Pacific salmon bilateral asymmetry of branchiostegals, in which the left side overlaps the right anteriorly and contains more rays, has been described by Jordan and Evermann (1896:479).

As a consequence of these known asymmetries in fish, morphological characters from both sides of all species, ideally, should be examined for taxonomic and racial studies, or examination should be limited to one chosen side. If the latter alternative has been adopted, problems arise if the chosen side is mutilated or otherwise unobtainable. In racial studies on Pacific salmon (Fukuhara et al., 1962), data on various meristic characters were arbitrarily collected from the left side of all specimens. The racial study involved multivariate analysis of data from several meristic characters; therefore occasional failures to obtain information from any one lost or damaged character prevented the specimen's

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use and reduced the usable sample size. As the reliability of the analysis was in part determined by the sizes of samples, unusable specimens were both a statistical and an economic loss.

Whether asymmetrical development, as shown in the branchiostegals of Pacific salmon, extends in some degree to other paired structures is unknown. With knowledge of the presence and extent of asymmetries in the characters considered, the opposite member of a lost character in fish specimens many times could be reliably substituted; if it were known that such characters essentially developed symmetrically, substitution would not contribute to the observed variability.

This paper presents an analysis of differences between the numbers of elements in left and right side structures of four paired meristic characters of sockeye (*Oncorhynchus nerka*), chum (*O. keta*) and pink (*O. gorbuscha*) salmon. In conjunction with this study, the reliability of the criteria utilized in obtaining the morphological characters will be discussed. The objectives of the analysis were to determine: (1) if bilateral asymmetry occurs in these characters; (2) the extent of asymmetries; (3) the direction of the asymmetrical development, as shown by one side tending to have a larger number of elements; and (4) the usefulness of the information in taxonomic and racial studies of the three species.

SAMPLES

Paired meristic characters were randomly obtained from specimens collected during the years 1956–1959 in the North Pacific Ocean, the Bering Sea, and from several North American and Kamchatkan rivers for racial studies conducted at the Seattle Biological Laboratory, Bureau of Commercial Fisheries. The characters examined included: (1) lateral line scales, (2) total gill rakers, (3) branchiostegal rays, and (4) pectoral fin rays. Lateral line scales of pink salmon were not examined because of extreme difficulty in obtaining reliable counts of the characteristically very small scales.

COLLECTION OF CHARACTERS

The paired bony structures were dissected from the specimens and left and right sides were radiographed separately. When the radiographs did not provide adequate resolution, the structure was stained and cleared, and the elements were counted manually. The data were obtained using criteria developed by Fukuhara et al. (1962: 27–28) for enumeration of characters. The definitions of criteria, elaborated upon below, include discussion of some structural characteristics and aberrancies which must be taken into account during enumeration of the characters. Application of these criteria minimized differences between individual interpretations and the time required for enumeration of the characters. As measured by periodic tests of between-reader variability, disagreements on independently obtained counts from radiographs averaged less than 3% for the bony characters. All scale counts were obtained by one biologist. Within-counter variability averaged less than 2%.

Lateral Line Scales

This character consisted of scales or scale pockets distinguishable by a tube which penetrates the scale and extends into the underlying lateral line canal. The count included the first scale posterior to the pectoral girdle and succeeding scales terminating at a position on the lateral line corresponding to the posterior margin of the hypural plate. This margin was determined by an incision made in the crease that resulted from upward flexion of the caudal fin. A severed scale or pocket was counted if more than half lay anterior to the incision. In immature specimens, acute scale imbrication required scale removal for accurate enumeration. Occasional irregularity of typically diagonal scale rows was caused by a supernumerary scale lying on the lateral line between two scales in the proper rows (Fig. 1). Some of these small scales lacked a tube and therefore were not counted.

Total Gill Rakers

This character consisted of rakers on the dorsal and ventral arms of the first branchial arch, including the most anterior rakers, which were

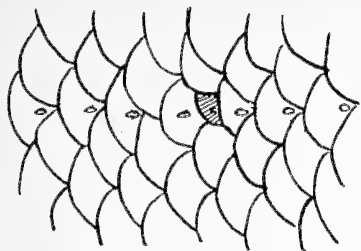


FIG. 1. Supernumerary scale lying on lateral line. Occasionally such scales are not penetrated by a lateral line canal tube.

frequently rudimentary. Rudimentary rakers occurring between the typically uniformly spaced rakers (Fig. 2a) and those lying outside the main row were not enumerated. Bifurcated or branched rakers (Fig. 2b) with a common base were counted as one raker.

Branchiostegal Rays

All bony elements of the branchiostegal were included in counts of this character. In chum salmon, particularly, the reduced size and modified shape of some anterior rays (Fig. 3) resulted in very deceptive radiographic presentations. In preparation for radiographing, the skin and cartilaginous material anterior to these rays had to be carefully removed to minimize deception. Careful examination was also required for recognition of an occasional ray which appeared as two rays due to the presence of a prominent lengthwise suture. Dissection and staining were used to resolve doubtful conditions.

Pectoral Fin Rays

All fin rays which extended to the basal bones of the fin were included in the character. So-called "floating rays," which occurred in various positions among the normal rays, were not counted (Fig. 4a). No counts were taken from fins in which a lateral process arising from one position had fused with a process on the opposite side arising either anterior or posterior to it. This left both a right and a left side process standing alone, as shown in Figure 4b.

STATISTICAL PROCEDURES

For each character, the right side counts were subtracted from the left side, differences being

positive when the left side counts exceeded the right and negative when the right side counts exceeded the left. The significance of the mean difference between the number of meristic elements in left and right side structures observed in each sample was determined using the Student's *t*-distribution:

$$t = (X - \mu) / S_x$$

where *X* equals the mean difference of left side counts minus those from the right side, μ equals zero, and *S_x* is the standard error of the sample mean difference. The hypothesis tested was that the difference between left and right side counts was zero. The hypothesis was rejected at the 0.05 level. The probability levels of the observed *t*-values are presented in the tables of data and results.

The extent of over-all asymmetry in each character was measured by the percentage $100(L + R)/N$, and the direction of asymmetry by the percentage of sinistrality $100L/(L + R)$, where *L* equaled the number of specimens with greater left side counts, *R* equaled the number with greater right side counts, and *N* equaled the total sample size, including specimens with equal numbers of elements in the left and right side structures.

Although there was little or no known biological reason to suspect that differential asymmetrical development was related to sex or area of origin of salmon, these possibilities were explored, in so far as the data warranted, for any obvious tendencies of this nature. Actual statis-

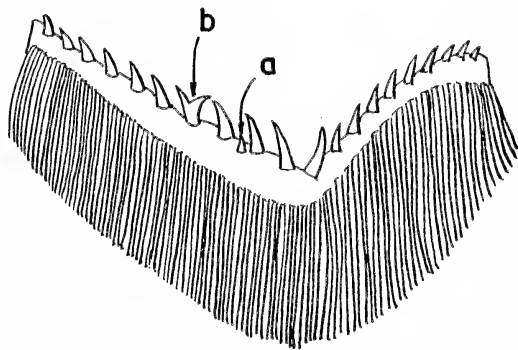


FIG. 2. First left gill arch. *a*, Small raker between regularly spaced rakers on ventral arm of the arch; *b*, a bifurcated raker on the ventral arm.

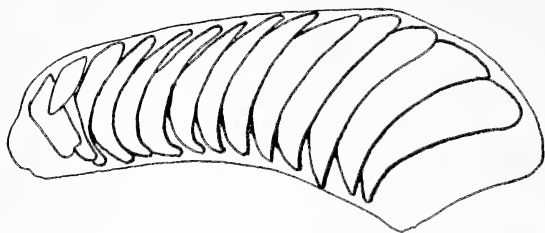


FIG. 3. Chum salmon branchiostegal, showing modified configuration of anterior rays.

tical analyses of between-sex, within-sample, differences were not attempted due to small sample sizes; nor were between-area differences tested for statistical significance, inasmuch as many samples were obtained from the high seas and contained specimens of unknown and perhaps differing origins.

For each sample, probability values associated with the *t*-distribution for differences between paired counts were obtained by sex. Sexes were then combined and analysed as a single sample. Similarly, for each species, probability values were determined for all males and females separately; the sexes were then combined to determine the mean differences between left and right side structures for comparison among species.

RESULTS

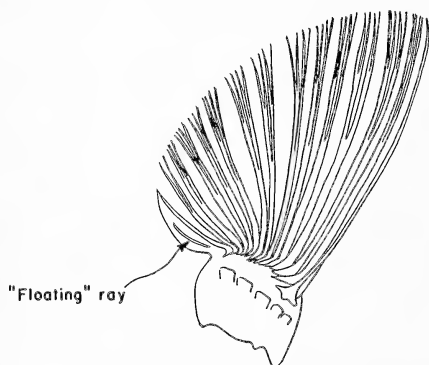
The results of the analyses of observed differences between left and right side structures are discussed for each meristic character. The occurrence, direction, and significance of the

mean differences between left and right side counts have been examined by species, sample location, and sex.

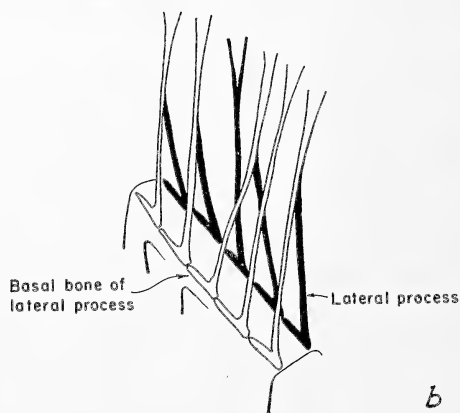
Bilateral Variation in Lateral Line Scales

In sockeye salmon (Table 1), the percentages of specimens exhibiting asymmetry in lateral line scales and the direction of asymmetry varied among samples of each sex and among combined samples of both sexes from different locations. As shown by the right-hand column (headed 100 P), the probability values for the observed mean differences were not significant. For the combined samples, males with differences in left and right side counts averaged 69%, and females averaged 65%. Asymmetry between left and right side scale counts occurred in approximately 67% of the total of 395 specimens. The direction of asymmetry indicated that the right side developed approximately 0.12 scales more than the left side. This difference could have occurred by chance alone more than 5 out of 100 times (*P* greater than 5); thus, the left and right side variations in lateral line scale counts were not significantly different in sockeye salmon.

Examination of data from chum salmon scale counts (Table 1), by sample location and sex, indicated some disparity among samples within these categories. Mean differences between left and right side counts of males were significant in one sample from the high seas. In this sample, collected by the MV "Paragon," the mean difference for females was not significant. In the Hokkaido Island sample both males and females



a



b

FIG. 4. Schematic presentations of aberrancies occurring in pectoral fins. *a*, "Floating" ray; *b*, fusion of lateral processes from adjacent fin ray bases.

TABLE 1
BILATERAL VARIATION IN THE NUMBER OF LATERAL LINE SCALES

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMET- RICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L-R)	100 (P)
MV "Attu" 56°N, 173°W (1957)	sockeye	male	13	69.2	66.7	0.307	> 50
		female	38	65.8	56.0	0.053	> 50
		total	51	66.6	58.8	0.118	> 50
	sockeye	male	32	68.8	50.0	-0.031	> 50
		female	19	63.2	33.3	-0.579	> 50
		total	51	66.6	42.8	-0.235	> 50
	sockeye	male	11	72.7	37.5	0	—
		female	24	62.5	66.5	0.208	> 40
		total	35	65.7	56.5	0.142	> 50
Okanogan River (1957)	sockeye	male	11	90.9	50.0	0	—
		female	13	76.9	50.0	0.154	> 50
		total	24	83.3	50.0	0.083	> 50
Japanese Fishery 50°N, 168°E (1958)	sockeye	male	61	59.0	41.6	-0.197	> 10
		female	54	68.5	43.2	-0.241	> 10
		total	115	63.4	42.4	-0.217	> 5
	sockeye	male	49	75.6	44.1	-0.244	> 10
		female	74	62.2	43.4	-0.175	> 10
		total	119	67.2	43.7	-0.202	> 10
Combined sockeye samples		male	173	68.8	46.2	-0.116	> 10
		female	222	65.3	47.6	-0.126	> 10
		total	395	66.8	47.0	-0.122	> 5
MV "Pioneer" 50°-53°N, 175°-180°W (1957)	chum	male	41	75.6	41.9	-0.341	> 10
		female	33	72.7	20.8	-1.121	< 1
		total	74	74.3	32.7	-0.689	< 1
MV "Paragon" 50°-60°N, 175°W (1957)	chum	male	72	76.3	36.3	-0.430	< 5
		female	63	84.1	52.8	0.111	> 50
		total	135	80.0	44.4	-0.178	> 10
Hokkaido I. (1958)	chum	male	109	70.6	25.9	-0.670	< 1
		female	51	72.5	35.1	-0.608	< 2
		total	160	71.2	28.9	-0.650	< 1
Combined chum samples		male	222	73.4	32.5	-0.532	< 1
		female	147	77.6	40.4	-0.415	< 2
		total	369	75.1	35.7	-0.485	< 1

showed significant differences in counts from opposite sides. Approximately 78% of the total female chum salmon samples exhibited asymmetrical development, while only 73% of the males were asymmetrical. However, the probability levels for the mean differences between sides for both males and females were not significant. Scale counts from the combined total of 369 chum salmon indicated some asymmetrical development in 75% of the specimens. Of all the specimens with asymmetries, counts from the right sides exceeded the left in approximately 64%. The over-all mean difference be-

tween left and right side counts (-0.485) was significant at the 0.01 level.

Bilateral Variation in Gill Rakers

Gill raker counts from the first left and right branchial arches were collected from sockeye salmon taken at 10 locations (Table 2). Male and female groups varied similarly, with no significant values occurring in either category in the individual samples. Probability values for sexes combined were significant in samples from 3 locations. Bilateral asymmetry occurred in approximately 63% of the total of 668 sock-

TABLE 2

BILATERAL VARIATION IN THE NUMBER OF GILL RAKERS

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMET- RICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L-R)	100 (P)
Nichiro 50°-53°N, 160°-178°E (1956)	sockeye	male	70	58.6	58.5	.228	>10
		female	93	63.4	59.3	.172	>10
		total	163	61.3	59.0	.196	< 5
Karluk River (1957)	sockeye	male	35	68.6	66.6	.343	> 5
		female	15	46.7	71.4	.200	>40
		total	50	62.0	67.7	.300	> 5
Naknek River (1957)	sockeye	male	12	66.7	75.0	.500	>10
		female	12	66.7	75.0	.583	> 5
		total	24	66.7	75.0	.542	< 5
Egegik River (1957)	sockeye	male	18	55.6	40.0	-.056	>50
		female	23	65.2	60.0	.130	>40
		total	41	60.9	52.0	.049	>50
Kvichak River (1957)	sockeye	male	12	75.0	66.6	.250	>20
		female	18	50.0	66.6	.278	>20
		total	30	60.0	66.6	.268	>10
MV "Tordenskjold" 51°N, 170°W (1959)	sockeye	male	31	67.7	47.6	-.194	>10
		female	41	70.7	44.8	-.146	>10
		total	72	69.4	46.0	-.167	>10
52°N, 172°W (1959)	sockeye	male	17	88.2	66.7	.530	>10
		female	10	60.0	33.3	-.200	>50
		total	27	77.8	57.1	.259	>10
56°N, 170° W (1959)	sockeye	male	51	66.7	50.0	-.059	>40
		female	42	66.7	64.3	.333	>10
		total	93	66.7	56.4	.118	>10
51°N, 180°W (1959)	sockeye	male	22	59.1	61.5	.454	>10
		female	15	46.7	85.7	.533	> 5
		total	37	54.1	70.0	.486	< 5
USSR: Ozernaya River (1959)	sockeye	male	46	56.5	57.7	.174	>10
		female	85	60.0	51.0	0	—
		total	131	58.8	53.2	.061	>50
Combined sockeye samples		male	314	64.0	57.7	.172	< 1
		female	354	61.9	57.5	.136	< 5
		total	668	62.9	57.6	.153	< 1
MV "Celtic" 50°-57°N, 145°-154°W (1956)	chum	male	41	46.3	21.1	-.366	< 1
		female	29	62.1	44.4	-.172	>10
		total	70	52.8	32.4	-.286	< 1
Ketchikan (1959)	chum	male	11	27.3	33.3	-.090	>50
		female	9	77.8	71.4	.333	>10
		total	20	33.0	60.0	.100	>50
USSR: Ozernaya River (1959)	chum	male	63	61.9	43.6	-.111	>40
		female	39	51.3	45.0	-.027	>50
		total	102	57.8	44.1	-.078	>40
Bolshaya River (1959)	chum	male	22	63.6	50.0	.045	>50
		female	67	58.2	51.3	.015	>50
		total	89	59.6	50.9	.022	>50
Okhotsk River (1959)	chum	male	29	44.8	61.5	0	—
		female	42	47.6	40.0	-.119	>30
		total	71	46.5	48.5	-.070	>30

TABLE 2 (continued)

Combined chum samples		male	166	53.0	42.0	-.138	> 5
		female	186	55.9	48.1	-.038	>50
		total	352	54.5	45.3	-.085	> 5
Petersburg (1959)	pink	male	37	54.0	60.0	.027	>50
		female	18	72.2	61.5	.111	>50
		total	55	60.0	66.6	.054	>50
Fraser River (1959)	pink	male	31	64.5	60.0	.064	>50
		female	18	50.0	55.6	.056	>50
		total	49	59.2	58.6	.061	>50
Combined pink samples		male	68	58.8	60.0	.044	>50
		female	36	61.1	59.1	.083	>50
		total	104	59.6	59.7	.058	>50

eye salmon examined. Of specimens exhibiting asymmetry, 58% had larger left side counts. In the combined data for the species, left side counts exceed the right by 0.15 rakers, which was significant at the 0.01 level.

In chum salmon (Table 2), the mean differences between left and right side gill raker counts were significant for only one sample collected on the high seas in 1956. Mean differences and probability levels varied among the samples of both males and females, with no apparent evidence of sexual dimorphism. The probability level for the mean differences calculated for all males combined was greater than 5%, and for all females was greater than 50%. Of the total of 352 pairs of chum salmon gill raker counts, 54% showed asymmetrical development of the structures. Asymmetry was toward the right side, which averaged 0.085 more rakers in these specimens; however, this difference was not significant.

In pink salmon (Table 2), differences between left and right side gill raker counts varied little among the categories of sample location or sex. In this species, 59% of the males and 61% of the females examined showed some asymmetry in gill raker counts from opposite sides of the fish, with a slight but consistent tendency for the left side to exceed the right. The probability levels for the samples and for all specimens combined, however, indicated that the observed mean differences were not statistically significant.

Bilateral Variations in Branchiostegal Rays

Pairs of branchiostegal ray counts were collected from 407 sockeye, 350 chum, and 59 pink

salmon (Table 3). Although very few specimens of pink salmon were examined, in this species, as well as in the other two, the females exhibited a greater percentage of asymmetrical development, with larger mean differences than the males. Only in sockeye samples from the Karluk and Egegik rivers, and in one chum salmon sample taken by the MV "Celtic," was the trend reversed. The mean differences observed were significant for all individual samples and also for each sample of male or female fish. In the combined data for each of the three species, asymmetrical development occurred in 62%, 77%, and 71% of the sockeye, chum, and pink salmon, respectively. Left side counts exceeded right side counts in 93% of the asymmetrical pairs of sockeye salmon branchiostegals, in 96% of the chums, and in 98% of the pink salmon. In sockeye salmon, the number of branchiostegal rays in the left side structures exceeded the right by approximately 0.6 rays; in chum and pink salmon the mean differences averaged 0.8 rays. The mean differences in all three species were statistically significant.

Bilateral Variation in Pectoral Fin Rays

Comparisons were made of fin ray counts from left and right pectoral fins of 407 sockeye, 357 chum, and 97 pink salmon (Table 4). No consistent trends were observed toward sexual dimorphism or effect of sampling location in respect to asymmetry of this character. For the combined data for each species, asymmetry occurred in only 14-24% of the specimens—much less frequently than for the other three characters examined. Variations in the number of rays from opposite sides resulted in very

TABLE 3

BILATERAL VARIATION IN THE NUMBER OF BRANCHIOSTEGAL RAYS

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMET- RICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L-R)	100 (P)
Nichiho 50°-53°N, 160°-178°E (1956)	sockeye	male	41	61.0	80.0	.415	< 1
		female	72	54.2	87.0	.472	< 1
		total	113	56.6	84.0	.451	< 1
Karluk River (1957)	sockeye	male	35	60.0	90.0	.543	< 1
		female	15	46.7	100.0	.533	< 1
		total	50	56.0	89.0	.540	< 1
Naknek River (1957)	sockeye	male	14	64.3	100.0	.857	< 1
		female	18	77.8	100.0	.889	< 1
		total	32	71.9	100.0	.875	< 1
Egegik River (1957)	sockeye	male	22	81.8	94.0	.818	< 1
		female	24	70.8	100.0	.750	< 1
		total	46	76.1	97.0	.783	< 1
Kvichak River (1957)	sockeye	male	13	38.5	100.0	.385	< 5
		female	16	87.5	100.0	.938	< 1
		total	29	65.5	100.0	.690	< 1
Ozernaya River (1959)	sockeye	male	46	52.2	95.8	.522	< 1
		female	91	65.9	95.0	.659	< 1
		total	137	61.3	95.2	.613	< 1
Combined sockeye samples		male	171	59.6	91.2	.556	< 1
		female	236	64.0	94.7	.640	< 1
		total	407	62.2	93.3	.604	< 1
MV "Celtic" 50°-57°N, 145°-154° W (1956)	chum	male	39	76.9	73.6	.820	< 1
		female	31	80.6	96.0	.774	< 1
		total	70	78.6	94.5	.800	< 1
Ketchikan (1959)	chum	male	13	76.9	100.0	.923	< 1
		female	9	77.8	100.0	1.333	< 1
		total	22	77.2	100.0	1.090	< 1
Ozernaya River (1959)	chum	male	58	75.9	90.9	.655	< 1
		female	39	92.3	100.0	.974	< 1
		total	97	82.5	95.0	.784	< 1
Bolshaya River (1959)	chum	male	24	70.8	88.2	.625	< 1
		female	67	77.6	100.0	.900	< 1
		total	91	75.8	97.1	.824	< 1
Okhotsk River (1959)	chum	male	29	62.1	94.4	.552	< 1
		female	41	73.2	100.0	.854	< 1
		total	70	68.6	97.9	.728	< 1
Combined chum samples		male	163	73.0	92.4	.693	< 1
		female	187	80.2	99.3	.904	< 1
		total	350	76.8	96.3	.806	< 1
Ketchikan (1959)	pink	male	31	67.7	95.2	.677	< 1
		female	28	75.0	100.0	.893	< 1
		total	59	71.2	97.6	.780	< 1

TABLE 4
BILATERAL VARIATION IN THE NUMBER OF PECTORAL FIN RAYS

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMET- RICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L-R)	100 (P)
Nichiro 50°-53°N, 160°-178°E (1956)	sockeye	male	40	25.0	60.0	.075	>40
		female	69	21.7	53.3	.014	>50
		total	109	22.9	56.0	.037	>40
Karluk River (1957)	sockeye	male	36	19.4	57.1	.028	>50
		female	16	31.2	40.0	-.062	>50
		total	52	23.0	50.0	0	—
Naknek River (1957)	sockeye	male	14	42.8	16.6	-.286	>10
		female	17	29.4	60.0	.059	>50
		total	31	35.4	36.3	-.097	>20
Egegik River (1957)	sockeye	male	22	22.7	40.0	-.045	>50
		female	23	13.0	66.7	.043	>50
		total	45	17.7	50.0	0	—
Kvichak River (1957)	sockeye	male	13	15.3	50.0	0	—
		female	18	16.6	33.3	-.056	>50
		total	31	16.1	40.0	-.032	>50
Ozernaya River (1959)	sockeye	male	47	17.0	75.0	.085	>10
		female	92	22.8	57.1	.022	>30
		total	139	20.9	62.1	.058	>20
Combined sockeye samples		male	172	22.1	52.6	.017	>50
		female	235	22.1	53.8	.021	>40
		total	407	22.1	53.3	.019	>40
MV "Celtic" 50°-57°N, 145°-154°W (1956)	chum	male	41	31.7	46.1	-.024	>50
		female	31	29.0	44.4	-.032	>50
		total	72	30.5	45.4	-.027	>50
Ketchikan (1959)	chum	male	13	23.0	66.7	.076	>50
		female	10	40.0	75.0	.200	>10
		total	23	30.4	71.4	.130	>10
Ozernaya River (1959)	chum	male	62	19.4	41.6	-.032	>50
		female	38	15.8	83.3	.105	>10
		total	100	18.0	55.6	.020	>50
Bolshaya River (1959)	chum	male	23	13.0	66.7	.043	>50
		female	68	23.5	75.0	.118	>20
		total	91	20.9	73.7	.099	>20
Okhotsk River (1959)	chum	male	29	10.3	66.7	.034	>50
		female	42	16.7	57.1	.024	>40
		total	71	14.1	60.0	.028	>50
Combined chum samples		male	168	23.8	50.0	-.006	>50
		female	189	22.2	66.7	.074	>50
		total	357	21.3	59.2	.036	>50
Ketchikan (1959)	pink	male	38	13.2	60.0	.026	>50
		female	12	16.7	100.0	.166	>20
		total	50	14.0	71.4	.060	>20
Prince William Sound (1959)	pink	male	40	15.0	66.7	.050	>50
		female	7	42.8	00.0	-.428	>10
		total	47	19.1	44.4	-.021	>50
Combined pink samples		male	78	14.1	63.6	.042	>10
		female	19	26.3	40.0	-.053	>50
		total	97	16.5	56.2	.021	>50

small mean differences for all three species; the mean differences for sockeye and pink salmon were approximately 0.02 and for chums 0.04. Although the left pectoral fin counts generally exceeded the right, the tests for differences were not statistically significant for any sample or species.

CONCLUSIONS

The results of this study show that sockeye, chum, and pink salmon, which are essentially bilaterally symmetrical animals, exhibit some asymmetries with respect to all four paired meristic characters considered. From the specimens examined no conclusive relationship was shown between the occurrences of asymmetries and the sex or the area from which samples were obtained; however, these possible sources of variation were not rigidly tested, for reasons given earlier in the text.

In taxonomic and racial studies involving lateral line scale counts, interchanging counts from left and right sides of chum salmon introduces an additional source of variation and, in a situation of considerable numbers of substitutions, may be a serious source of bias. In sockeye salmon, substitution of one side for another appears feasible; however, variation in the probability levels of individual samples suggests that, for more complete assurance of reliability, examination of a larger number of sockeye salmon specimens would be desirable.

Substitution of gill raker counts from sockeye salmon is not advisable. In chum salmon the observed differences in left and right side counts are not statistically significant; however, the differences observed in one high seas sample containing 70 specimens raise some doubt in situations in which loss of a character, resulting in reduced sample size, is a lesser problem than

maintaining minimum variations in the data to be collected. Gill raker counts from opposite sides of pink salmon vary equally, and substitution of the opposing structure will not seriously affect the analysis.

In the species considered, branchiostegal counts from left and right sides can not be reliably interchanged. Also, the extent of the asymmetry observed in this character is of a greater magnitude in female salmon. Further study of sexual differences in left and right side variations is required, however, to yield conclusive evidence of the existence of sexual dimorphism in respect to bilateral variations in branchiostegals of Pacific salmon.

Pectoral fin rays from the left and right side structures are essentially equal in number in all three species. Substitution of sides in obtaining counts of pectoral fin rays would contribute little variation to mean counts of this character.

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Notes on Indo-Pacific Scleractinian Corals, Part 4

A Second Species of *Stylocoeniella*

JOHN W. WELLS¹

In 1890 P. W. Bassett-Smith described a new species of *Stylophora*, *S. guentheri*, from two specimens dredged on the Macclesfield Bank, China Sea. His description (1890:362), although unaccompanied by a figure, is of a form so distinct that it cannot be confused with other species of this genus. To the writer's knowledge this species has not been subsequently noticed or referred to. In 1955 an encrusting colony of a *Stylophora*-like form was collected at Eniwetok Atoll (Marshall Islands) by R. T. B. Iversen in the course of making a reference collection for the Eniwetok laboratory. At the time, the writer thought it might be a new species but hesitated because of the possibility that it might be merely the expanded base of one of the species of the normally ramose *Stylophora*. More specimens of the same coral were collected at Eniwetok lagoon in 1960 by E. J. Kuenzler and L. R. Pomeroy, and in the summer of 1964 P. Spencer Davies collected several more at Addu Atoll (Maldive Islands).

From the consistently encrusting growth habit and other characters it is now clear that these specimens represent a species quite different from the common forms of *Stylophora*, such as *S. pistillata* and *S. mordax*, and that Bassett-Smith's recognition of its distinctness was correct, although its relationships appear to be with *Stylocoeniella* rather than *Stylophora*.

The writer expresses his thanks to Dr. W. J. Rees of the British Museum (N.H.) for providing photographs of the type specimen of *S. guentheri* and to Dr. P. Spencer Davies of Glasgow University for permission to use material collected by him.

Family ASTROCOENIIDAE

This familial epithet is used here in a broad sense pending modifications in its scope that will

develop as the relationships of the genera now included in it are better known. *Stylocoeniella* is certainly closely allied to *Actinastrea*, and both genera are nearer to the Pocilloporidae than to the stylocoeniid corals.

Genus *Stylocoeniella* Yabe and Sugiyama 1935

TYPE SPECIES: *Stylocoenia banzawai* Y. and S. 1933 = *Stylophora armata* Ehrenberg 1834.

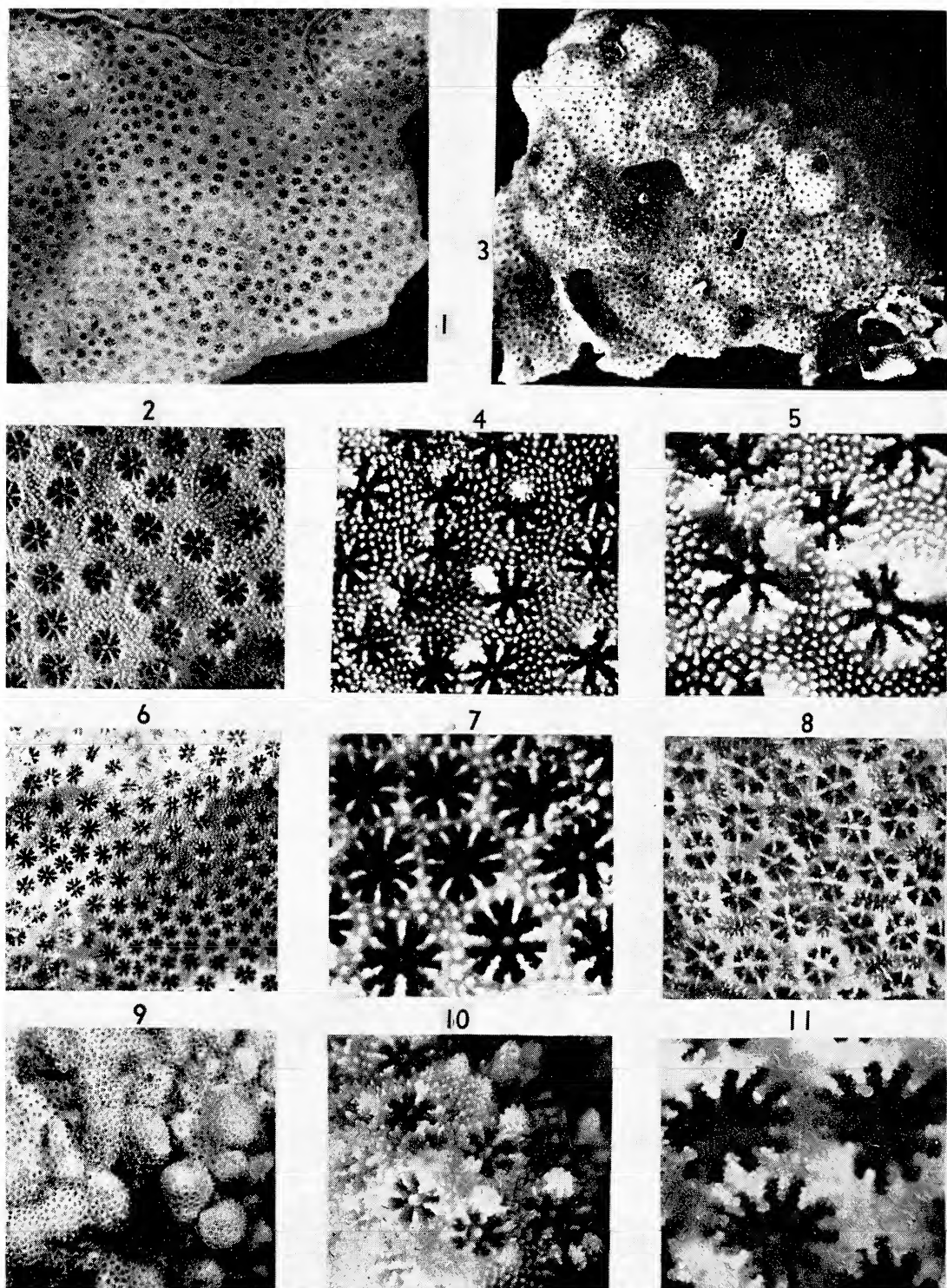
Stylocoeniella guentheri (Bassett-Smith) 1890
Figs. 1-10

Stylophora guentheri Bassett-Smith 1890.
Ann. Mag. Nat. Hist. (6), 6:362.

? *Stylocoeniella* sp. Wells 1964. U. S. Geol. Surv. Prof. Paper 260-DD:1103, pl. 296, figs. 6, 7.

Corallum thin (1-7 mm), encrusting, with basal epitheca. Corallites generally plocoid, cylindrical, 0.5-1 mm apart, united by solid or vesicular coenosteum the surface of which is covered with evenly spaced, minutely granulated spines, 10-15/mm (Figs. 2, 4, 5), but occasionally cerioid (Figs. 6, 7) with closely fused walls where crowded. New corallites arise by extratentacular budding on the surface of the coenosteum between corallites. Calices circular except where crowded and polygonal (cerioid), 0.5-0.75 mm in diam, margins flush with surface of coenosteum. Septa 12 in number, the 6 septa of the first cycle well developed, slightly exsert peripherally, relatively thick and extending from the corallite wall about half way to the axis, their inner edges dropping abruptly to join the columella deep in the calice. The margins of the primary septa bear four or five coarse dentations (Fig. 5), the terminations of trabeculae inclined upward and inward from the wall. In nearly all corallites the outer upper margin of one of the primary septa is elevated

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FIGS. 1-10. *Stylocoeniella guentheri* (Bassett-Smith). 1 and 2, Portions of holotype (B.M.N.H.1889.9.24.-84), 58 m, Macclesfield Bank, $\times 2$, $\times 6$; 3, 4, and 5, corallum and calices, lagoon, 15 m, Gan I., Addu Atoll, $\times 1$, $\times 10$, $\times 15$; 6 and 7, calices, lagoon, 40 m, Eniwetok Atoll, $\times 4$, $\times 15$; 8, calices, lagoon, 4 m, Eniwetok, $\times 10$; 9 and 10, portion of corallum and calices, lagoon, 6 m, Gan I., Addu Atoll, $\times 1$, $\times 10$.

FIG. 11. *Stylocoeniella armata* (Ehrenberg). Calices (compare with Figs. 5 and 7), 0.5 m, Heron I., Great Barrier Reef, $\times 15$.

into a prominent, thickened, laterally striated and granulose spine (Figs. 4, 5, and 10), the external base of which may carry up the spinose coenosteum. The second cycle of septa is weakly developed, each septum consisting of a row of fine trabecular spines projecting nearly horizontally inward from the wall and extending about a quarter of the distance to the axis. Columella a prominent solid style rising to the level of the calice rim or slightly exsert (Figs. 5 and 8).

The encrusting rather than ramose growth habit and dentate septa easily distinguish this species from *Stylophora*, but otherwise it has all the characters of that genus: small corallites, few septa, styliform columella, spinose vesicular, tabular, or solid coenosteum, and styliform effusions from one of the primary septa (more columniform in *S. guentheri* than the "hoods" of *Stylophora*). The dentation of the septa is perhaps the most important difference, although the primary septa of *Stylophora* may show traces of such structures, and *S. guentheri* is best placed in *Stylocoeniella* next to the type species *S. armata*, with which it shares the same growth form, styliform septal proliferations, and occurrence as inconspicuous patches on reefs and shallower parts of lagoons. In *S. armata*² (Fig. 11; see also Yabe and Sugiyama, 1935: Pl. 15, and Wells, 1954: Pl. 96, figs. 1–4) the calices are larger (0.75–1.25 mm), more nearly cerioid than plocoid, the 6 septa of the second cycle are more completely developed, frequently

nearly equal to the first cycle, and the trabecular dentation on the inner end of each primary septum adjacent to the columella is often large and paliform.

The fragmentary fossil specimen from the Miocene of Eniwetok recently referred by the writer to *Stylocoeniella* is indistinguishable from *S. guentheri* in all respects except for the slightly larger (1 mm) calices.

HOLOTYPE: British Museum (N.H.) No. 1889.9.24.84:58 m, Macclesfield Bank, China Sea.

DISTRIBUTION: Miocene (?) (Eniwetok). Recent: Macclesfield Bank, 40–58 m; lagoon, 4–40 m, Eniwetok Atoll; lagoon reef slope, 6–26 m, Gan I., Addu Atoll (Maldives Islands).

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² In addition to the previously reported occurrences of this species cited by the writer (1954:410; 1955), subsequent collections indicate its presence in Saipan, Ifaluk Atoll (Caroline Islands), Eniwetok and Arno Atolls (Marshall Islands), and Zamboanga (Philippines).

The Echinoidea Collected by the Royal Society of London Expedition to Southern Chile, 1958-1959

DAVID L. PAWSON¹

ABSTRACT: The collection comprises the species *Arbacia dufresnei* (Blainville), *Pseudechinus magellanicus* (Philippi), and *Loxechinus albus* (Molina). Typical temnopleurid epistroma is now known to be present in juveniles of *Pseudechinus magellanicus*, and the disposition of the ocular plates in the apical system in this species is determined by the position of the anal aperture. The shallow water echinoid fauna of southern Chile includes the endemic genera *Loxechinus* and *Tetrapyrgus*, and genera with antarctic (*Tripylus*) and circumpolar (*Pseudechinus*) affinities.

DURING LATE 1958 and early 1959, an expedition sponsored by the Royal Society of London conducted marine and terrestrial investigations in southern Chile. Littoral marine stations were established in three separate areas: (1) Isla Chiloë (approx. 42°S), (2) Puerto Eden to Punta Arenas (approx. 49°–52°S), and (3) Isla Navarino and southern regions (approx. 55°S).

The present paper contains an account of the Echinoidea collected in the intertidal and sublittoral zones by the expedition's marine biologist, Professor G. A. Knox, of Canterbury University, Christchurch, N.Z.

The collection contains 243 specimens which represent three genera and three species. The three species are common in southern Chile and are typical of that area. *Pseudechinus magellanicus* (Philippi) is abundant in the collection. It is a species of a southern genus which apparently originated in Australasia, and has spread to various subantarctic localities with the aid of the west wind drift. *Loxechinus albus* (Molina) is a large urchin with a green test and green spines and is used extensively as food in the areas in which it occurs. The third species, *Arbacia dufresnei* (Blainville), has a characteristic green test and purple spines.

I would like to thank Professor G. A. Knox

and the Royal Society for the opportunity to study this collection.

MATERIAL EXAMINED

Echinoids were collected at the following stations:

Stn. 19. Puerto Eden, Isla Wellington, 49°08'20"S, 74°26'55"W; intertidal granitic gneiss rocks, sheltered; hand collecting, also collection from *Macrocystis* fronds and holdfasts, and sublittoral collection by diving; Nov. 29–30, 1958. *Pseudechinus magellanicus*, 8 specimens.

Stn. 21. Puerto Eden, 49°08'30"S, 74°26'52"W; depth 16–18 m, grey sand; dredge; Dec. 2, 1958. *P. magellanicus*, 5 specimens.

Stn. 22. Puerto Eden, 49°08'48"S, 74°26'48"W; depth 6–8 m, grey sand with small stones; dredge; Dec. 2, 1958. *Arbacia dufresnei*, 1 specimen; *P. magellanicus*, 8 specimens.

Stn. 24. Puerto Eden, 49°08'31"S, 74°26'48"W; depth 10–12 m, grey sand; dredge; Dec. 4, 1958. *P. magellanicus*, 2 specimens.

Stn. 27. Isla Carlos, 49°09'35"S, 74°25'24"W; collection from *Macrocystis* fronds and holdfasts; Dec. 5, 1958. *A. dufresnei*, 1 specimen.

Stn. 29. Isla Carlos, Puerto Eden, 49°08'38"S, 74°25'32"W; intertidal gneiss rocks, semi-exposed; hand collecting; Dec. 6, 1958. *P. magellanicus*, 1 specimen.

¹ U. S. National Museum, Smithsonian Institution, Washington 25, D.C. Manuscript received November 17, 1964.

- Stn. 33. Puerto Eden, 49°09'28"S, 74°26'06"W; depth 11–12 m, sandy mud with *Mytilus* shell; dredge; Dec. 8, 1958. *P. magellanicus*, 17 specimens.
- Stn. 37. Caletta Lackawana, 49°10'32"S, 74°25'52"W; depth 18 m, sand rock, shell; dredge; Dec. 9, 1958. *P. magellanicus*, 1 specimen.
- Stn. 39. Puerto Eden, west side of Canal Sur, 49°09'52"S, 74°26'08"W; intertidal boulder beach of granitic gneiss; hand collecting and collection from *Macrocystis* fronds and holdfasts; Dec. 9–11, 1958. *A. dufresnei*, 6 specimens; *P. magellanicus*, 9 specimens; *Loxechinus albus*, 5 specimens.
- Stn. 40. Isla Dulce and Isla Levinson, Puerto Eden, 49°09'02"S, 74°25'10"W; intertidal and sublittoral granitic gneiss rocks; hand collecting; Dec. 12–13, 1958. *P. magellanicus*, 5 specimens.
- Stn. 44. Puerto Eden, 49°08'16"S, 74°25'34"W; depth 3–5 m sand; Dec. 18, 1958. *P. magellanicus*, 7 specimens.
- Stn. 49. Bahia Muñoz Gomera, 59°20'S, 73°32'W; intertidal basaltic rock; hand collecting and collection from *Macrocystis* holdfasts; Dec. 26, 1958. *P. magellanicus*, 1 specimen.
- Stn. 50. Puerto Williams, Isla Navarino, 54°55'40"S, 67°39'W; intertidal boulder beach; hand collecting; Jan. 7, 1959. *P. magellanicus*, 1 specimen.
- Stn. 51. Puerto Williams, Isla Navarino, 54°55'30"S, 67°34'30"W; intertidal argillite rocks; hand collecting and collection from *Macrocystis* fronds and holdfasts; Jan. 8, 24, 31, 1959. *P. magellanicus*, 6 specimens; *L. albus*, 2 specimens.
- Stn. 52. Puerto Robalo, Isla Navarino, 54°55'50"S, 67°41'40"W; intertidal argillite rock; hand collecting and collection from *Macrocystis* fronds and holdfasts; Jan. 10, 16, 23, 30, 1959. *A. dufresnei*, 3 specimens; *P. magellanicus*, 17 specimens.
- Stn. 57. Isla Hermite, Caleta San Martin, 55°51'S, 67°32'W; intertidal granitic rock; hand collecting; Jan. 13, 1959. *L. albus*, 1 specimen.
- Stn. 66. Puerto Williams, Isla Navarino, 54°55'35"S, 67°36'50"W; depth 2–4 m, grey mud with boulders; dredge; Jan. 22, 1959. *P. magellanicus*, 7 specimens.
- Stn. 68. Puerto Williams, Isla Navarino, 54°55'40"S, 67°36'50"W; depth 0–5 m; collection by diving; Jan. 29, 1959. *P. magellanicus*, 34 specimens.
- Stn. 70. Isla Bertrand, 55°14'30"S, 67°55'40"W; intertidal granitic rock, very exposed; hand collecting; Feb. 3, 1959. *L. albus*, 8 specimens.
- Stn. 73. Seno Grandi, small island opposite Puerto Grandi, 55°15'S, 67°56'W; collection from *Macrocystis* fronds and holdfasts; Feb. 5, 1959. *P. magellanicus*, 12 specimens.
- Stn. 74. Seno Grandi, peninsula on Isla Navarino opposite Puerto Grandi, 55°11'20"S, 67°56'W; collection from *Macrocystis* fronds and holdfasts; Feb. 5, 1959. *P. magellanicus*, 5 specimens.
- Stn. 75. Seno Grandi, point on Isla Navarino east of Rio Grande, 55°11'20"S, 67°52'30"W; intertidal volcanic rocks, sheltered; hand collecting; Feb. 5, 1959. *P. magellanicus*, 1 specimen.
- Stn. 77. Puerto Grandi, Isla Bertrand, to the west of the wharf, 55°12'S, 67°55'30"W; intertidal granitic rocks and boulder beach, semisheltered; hand collecting; 7/2/1959; collection by diving among *Macrocystis*; Feb. 8, 1959. *P. magellanicus*, 2 specimens.

ECHINOIDEA

Family ARBACIIDAE Gray, 1855

Arbacia Gray, 1835TYPE SPECIES: *Arbacia lixula* (Linnaeus).

REMARKS: This well-defined genus contains seven species, of which *A. dufresnei* (Blainville) and *A. spatuligera* (Valenciennes) are known from southern Chile. Unfortunately the latter species is not represented in the present collection.

Arbacia dufresnei (Blainville)

Fig. 1

Arbacia dufresnei Mortensen, 1935:579 (complete list of references); 1936: 215; 1952: 8; Bernasconi, 1935:12, pl. V, pl. VI, figs. 8-10, pl. VII, fig. 4, pl. VIII, figs. 7-11.

DIAGNOSIS: Denuded test green, radioles purple.

MATERIAL EXAMINED: 11 specimens, from Stn. 22 (1); Stn. 27 (1); Stn. 39 (6); Stn. 52 (3).

REMARKS: These are typical representatives of this well known and attractive species. The largest specimen has a horizontal diameter of 42 mm, and a height of 23 mm, while the smallest is 16 mm and 7 mm, respectively. Two specimens (both from station 52) carry reproductive products on the aboral side of the test. In one the products are eggs, and in the other, sperms. The presence of eggs and sperms on the test of *A. dufresnei* has also been observed by Studer (1880) and Mortensen (1936). A specimen from station 39 is unusual in possessing seven anal valves (Fig. 1), while members of the family Arbaciidae characteristically have four or five. This single variant is apparently normal in all other respects. Jackson (1927) has reported considerable variation in the anal valves in *Arbacia punctulata*, at least 10% of the 10,000 specimens he examined having more or less than four anal valves. It is possible that a similar degree of variation exists in *A. dufresnei*.

The characteristic green colour of the test is darker in smaller specimens.

DISTRIBUTION: *A. dufresnei* is known from the southern part of South America, from Rio de la Plata in the east to Puerto Montt in the west, Antarctica (Booth Wandell Island), and the Falkland Islands, in depths ranging from the intertidal zone to 315 m.

Family TEMNOPLEURIDAE Agassiz, 1872

Pseudechinus Mortensen, 1903

TYPE SPECIES: *Pseudechinus albocinctus* (Hutton).

REMARKS: Genus *Pseudechinus* contains twelve species, all of which have a southern distribution. Six of the species are apparently restricted to the New Zealand region.

Fell (1958, 1962) has discussed the systematic position of this genus, consequent upon his discovery of weakly developed epistroma in three of the New Zealand species, *P. flemingi* Fell, *P. albocinctus* (Hutton), and *P. novaezealandiae* (Mortensen). As the presence of epistroma is an important temnopleurid character, there is strong evidence for the retention of the genus in the Family Temnopleuridae. Mortensen (1943) had supplied some independent evidence in favour of this systematic position. No larval stages are yet known for this genus, but they should prove to be of the characteristic temnopleurid type.

Pseudechinus magellanicus (Philippi)

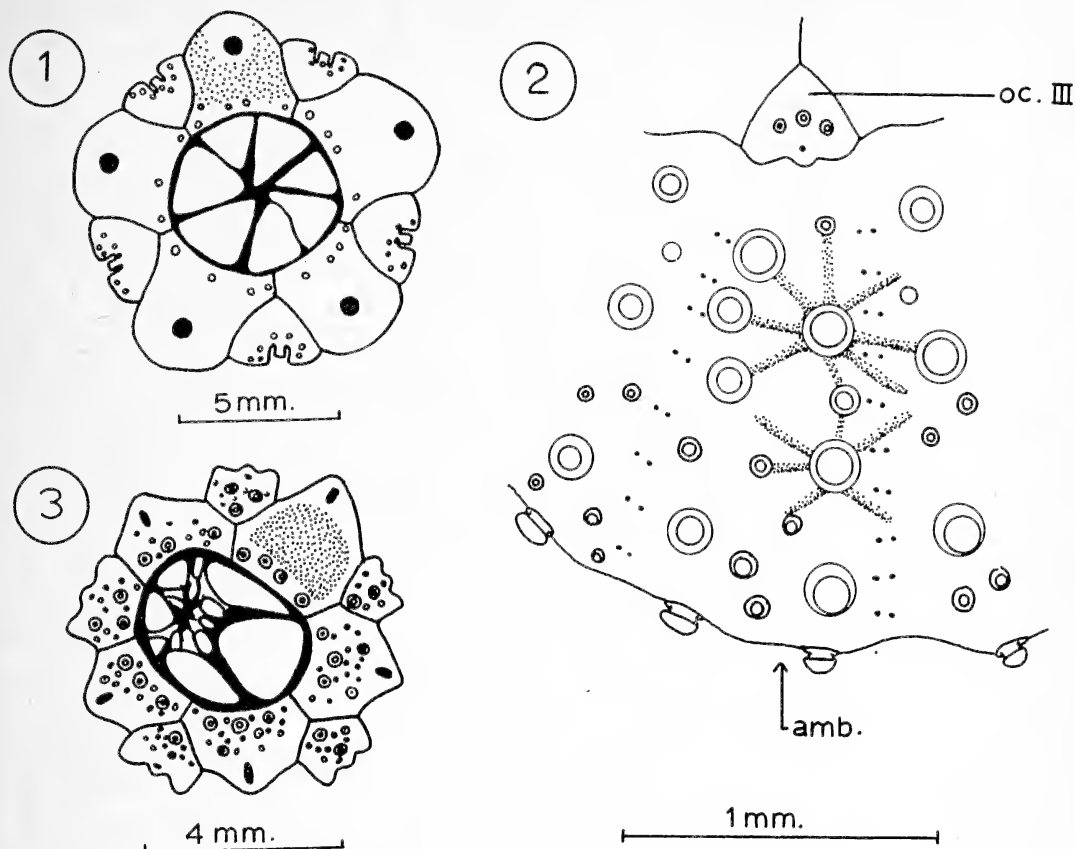
Figs. 2, 3

Pseudechinus magellanicus Mortensen, 1943: 232, figs. 125, 126a (complete list of references); 1952:9; Bernasconi, 1953:17, pl. VII, figs. 2-3, pl. VIII, figs. 1-6, pl. XVIII, figs. 3-4.

DIAGNOSIS: Denuded test faintly red, radioles light red. Tubercles finely crenulate. Valves of globiferous pedicellariae each with one or two lateral teeth. Apical system with ocular I insert. Suranal plate large, naked.

MATERIAL EXAMINED: 216 specimens, from Stn. 19 (8); Stn. 21 (5); Stn. 22 (8); Stn. 24 (2); Stn. 27 (67); Stn. 29 (1); Stn. 33 (17); Stn. 37 (1); Stn. 39 (9); Stn. 40 (5); Stn. 44 (7); Stn. 49 (1); Stn. 50 (1); Stn. 51 (6); Stn. 52 (17); Stn. 66 (7); Stn. 68 (34); Stn. 73 (12); Stn. 74 (5); Stn. 75 (1); Stn. 77 (2).

REMARKS: The smallest specimen has a horizontal diameter of 4 mm, while that of the largest is 29 mm. Two distinct size groups are represented, the first comprising those specimens with a diameter of 17-29 mm, and the second, those with a diameter of 4-10 mm. These probably represent two year-groups. Mortensen (1952) reported two size groups in a collection examined by him, but the groups comprised juveniles 2-5 mm in diameter and



FIGS. 1-3. *Arbacia dufresnei* and *Pseudechinus magellanicus*. 1, *A. dufresnei*, abnormal apical system with seven anal valves. 2, *P. magellanicus* juvenile, showing radiating epistomal ridges in an ambulacrum. 3, *P. magellanicus*, abnormal apical system with ocular IV insert. Abbreviations: amb., ambulacrum; oc. III, ocular III.

adults 12-15 mm in diameter. His material was collected in July, while the present specimens were collected between November and February.

The apical systems of 50 specimens were examined. A specimen 6 mm in diameter has two large suranal plates instead of the usual one, and these plates almost fill the periproctal space. In almost all cases, the anterior ocular plate (oc. III) is strongly exsert and oc. I is insert, while the anus tends to occupy a position posterior in the periproct, near oc. I. Some specimens show other ocular plates near the posterior end of the apical system to be almost insert (oc. II and V), while in a specimen of 27 mm h.d. oc. I and II are broadly insert and oc. V is almost insert. The fact that oc. III remains the most strongly exsert of all the ocular plates agrees with the observations made by Fell (1963) on

the tendency for the anus to migrate posteriorly, and the effects of this tendency on the plates of the apical system. Another specimen 23 mm in diameter has an unusual apical system (Fig. 3) in which only oc. IV is insert, and while the anus is as usual excentric, it does not lie in its normal posterior position, but nearest oc. IV. Oculars I, II, III, and V are here strongly exsert.

Small specimens were examined for traces of a temnopleurid epistroma, which has already been found in some other members of the genus *Pseudechinus* (see above). Epistroma is definitely present in *P. magellanicus*, at least in juvenile specimens. The smallest specimen in the collection (4 mm h.d.) shows weakly developed ridges radiating from the areoles of primary and secondary tubercles, especially in the ambulacra, near the apical system (Fig. 2).

The remainder of the area is sculptured, so that in this aboral region the median sutures of the ambulacral plates cannot be seen. Slightly larger specimens show faint traces of an epistroma, but these soon disappear as the animal grows. This parallels the situation in *P. novaezealandiae* and *P. albocinctus*, where the epistroma disappears before maturity is reached (Fell, 1958:36).

The stomach contents of several specimens consisted almost entirely of fragments of a brown alga, probably *Macrocystis*. This species appears to be predominantly a vegetarian browser.

DISTRIBUTION: *P. magellanicus* is well known from the southern part of South America. To the east the northern limit of its range is about 35°S (Rio de la Plata), and to the west the northern limit is about 41°S (Puerto Montt). The species also occurs at Tristan da Cunha. It is extremely common in some areas, and appears to favour life in the *Macrocystis* zone, where it may be found in large numbers on the fronds of *Macrocystis*.

Family STRONGYLOCENTROTIDAE Gregory,
1900

Loxechinus Desor, 1856

TYPE SPECIES: *Loxechinus albus* (Molina).

REMARKS: This genus is monotypic.

Loxechinus albus (Molina)

Loxechinus albus Mortensen, 1943:172 (complete list of references), pl. LVII, figs. 18-19; 1952:10; Bernasconi, 1953:23, pl. VII, fig. 1, pl. XI, pl. XII, figs. 1-9.

MATERIAL EXAMINED: 16 specimens, from Stn. 39 (5); Stn. 51 (2); Stn. 57 (1); Stn. 70 (8).

REMARKS: The largest specimen has a horizontal diameter of 82 mm and a height of 40 mm, and the smallest 23 mm and 13 mm, respectively. In all specimens the radioles are green, and the denuded test is faintly purple admedially in the ambulacra and interambulacra, green elsewhere.

DISTRIBUTION: This species is known to oc-

cur on the west coast of southern South America, as far north as Callao, Peru. While its depth range is 0-340 m, it is most commonly found in the littoral zone, where it may be extremely abundant.

DISCUSSION

In area 1 (Isla Chiloe, Stns. 1-19), no echinoids were collected, although Professor Knox (personal communication) noted the presence of a common sea urchin (probably *L. albus*) on the rocky coasts.

The three species in the collection were taken from the other two areas, Puerto Eden to Punta Arenas (Stns. 19-49) and Isla Navarino (Stns. 50-78), where they are all represented in the rocky infralittoral zone.

Species not represented in the collection, but known to occur in southern Chile, include the arbaciid *Tetrapygyus niger* (Molina) and the schizasterids *Tripylus excavatus* Philippi and *Tripylaster philippi* (Gray).

The known echinoid fauna of this region is related to the faunas of other subantarctic or cold temperate localities at the generic level. *Pseudechinus* is a southern genus, with species on many subantarctic islands. *Arbacia* appears to have the west coast of South America as its centre of distribution, whence species have spread to the east coast, and to the Atlantic coast of Africa (Mortensen, 1935). The genera *Loxechinus* and *Tetrapygyus* are monotypic, and their species are known only from the southwestern coast of South America. *Tripylus* has three species in the Antarctic seas, and a single species is known from the southern tip of South America. Tropical genera are not conspicuous in the shallow water fauna.

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Land Snails of Ulithi Atoll, Caroline Islands: A Study of Snails Accidentally Distributed by Man

HAROLD W. HARRY¹

DURING THE SECOND WORLD WAR I had occasion to visit briefly on Mogmog Islet, Ulithi Atoll, Western Caroline Islands, and to collect the land snails reported herein. The collection was divided, and one part, including all specimens of several less abundant species, was sent to the late Dr. C. Montague Cooke, Jr. of the Bernice P. Bishop Museum. In unsorted "sweepings" he found a few species which I had overlooked. It was his intention to publish the data in a paper on comparative faunal studies of the Mid-Pacific Islands, but death intervened. Some years later I had the opportunity to study more carefully the set I retained, using the extensive collection and library at the University of Michigan Museum of Zoology. More recently, a grant from the National Science Foundation (NSF GB-2753) has made it possible to complete the study.

The collection is significant in several ways. Although there have been very few papers on the nonmarine mollusca of the Pacific atolls, this fauna seems to be larger than any previously reported (Hedley, 1899; Pilsbry, 1900; Reigle, 1964; and the bibliography of the latter paper). Most if not all of the species are disseminated by man, thus providing not only an antithetical example of a fauna of high endemism, but also shedding new light on the vexing problem of zoogeography of the land snails of the Indo-Pacific area. The pitifully slow rate at which data on the Indo-Pacific land snails have accumulated has been due in large part to the inadequate descriptions and lack of illustrations of many species. The present study afforded opportunity to illustrate and redescribe several species thus neglected. Moreover, two species have interesting growth patterns which have not been previously reported, but which are of systematic importance.

¹ Texas A&M University Marine Laboratory, Galveston, and Rice University, Houston, Texas. Manuscript received February 23, 1965.

Mogmog Islet is one of several which inclose the lagoon of Ulithi Atoll. The closest islands to Ulithi (10° 5' N, 139° 43' E) are Fais, 45 miles to the east; Yap, 110 miles westward; and Guam, 400 miles to the north. Between World War I and World War II these islands had been a Japanese protectorate, as were the Marianas north of them, and the Palau Islands to the west. Several hundred Micronesians who called Mogmog home had been evacuated at the time of my visit. Writing at the turn of the century, Christian (1899:18-20) noted that there was a tradition of annual commerce between the Caroline Islands and Guam, carried on in native canoes. Also, the natives of Yap and Peleliu (in the Palau Islands) "used to go on long voyages of trading and conquest," and the natives of Ulithi "have from ancient times been subject to Yap, and they come down every February to pay them tribute."

Much of Mogmog Islet, which is only a few acres in extent, had been cleared of undergrowth when I visited it in August 1945. It was then being used as a recreational area for U. S. Navy personnel. The seaward margin of Mogmog is about 8 or 10 ft above the beach, which it fronts precipitously. From this meager elevation the land slopes gently down to the lagoon. Along the outer edge of the islet was a narrow strip of land on which the undergrowth was left relatively undisturbed. This zone was covered with large chunks of loose coral rock. The land snails were picked from the organic mulch which had collected between them. Near the center of Mogmog was a depression of about ½ acre, in which grew several species of emergent freshwater plants. The surface of this pond had been heavily oiled.

Besides the snails which I collected, a number of other land animals were in evidence. A species of terrestrial flatworm was abundant, and there was one species each of an isopod, a millipede, and a centipede. Of insects, I noted

at least four species of ants, several kinds of flies, a small cockroach, a locust, several beetles, a butterfly, and a moth, as well as dermaptera, isoptera, and homoptera (one scale insect was very common). Most surprising was the presence of mosquitoes and dragonflies, both of which require freshwater for the completion of their life cycles. There was also a small lizard (a skink) and one or more species of small forest birds.

Of plants, there were several species of broad-leaf trees as well as pandanus and a few other shrubs. But, to a nonbotanist, these were eclipsed by the overwhelming abundance of the coconut palm. Contrary to popular opinion, the coconut palm, which is ubiquitous throughout the Pacific islands at lower elevations, does not constitute a natural forest. It is probably not even native to the area. The coconut groves are entirely the result of being planted and maintained (at least through replanting) by human agency. More detailed discussion of this subject will be found in Hedley (1899), O. F. Cooke (1910), Taylor (1950), Bates (1956), and Wiens (1962). From this it follows that the atolls forested with coconut palms are essentially cultivated areas. Wiens (1962) cites quite a few other plants which are introduced and maintained by human agency on atolls.

Some pertinent excerpts from Dr. C. M. Cooke's letters to me follow:

A number of genera [from Mogmog] such as *Kororia*, *Nesopupa*, *Georissa*, and *Palaina* are rarely, if ever, found on a typical atoll. From the list of the genera, the fauna appears to be that of a raised atoll such as Fais. I might hazard the guess that Ulithi is slightly raised with the islets composed of hard coral limestone. In typical, low lying atolls the interior of the islet is made up entirely of coral rubble. These typical atolls have a very restricted fauna made up mostly of species that are accidentally distributed by man.

In 1941 we received a small collection from Fais. This island is east of Ulithi and about 65 feet high, with no lagoon. The genera and species of land shells coincide almost exactly with those we now know to inhabit Ulithi. Species from both these islands are quite distinct from those known to inhabit Yap.

In my work on the faunas of the Pacific Islands I have divided the islands into three types. First, the high volcanic islands. Some of these may be quite old. The shell fauna of these islands contain endemic genera, subgenera and many species. Hawaii, Samoa, the Marianas, and all the important groups belong to

this type. The lowland fauna may include many of the "wides" that are probably man-distributed. The second type is the raised coral island such as Fais in the Carolines; Makatea, Henderson, etc., in the Tuamotu. This type of island is not very old. They may have a few endemic species but not endemic genera. Quite a large portion of the fauna is man-distributed species. The third type of island is the low coral atoll. Some of these atolls may have as many as ten species but as the islands are apparently subjected to being washed over by hurricanes, all their shell species can be attributed to man's accidental introduction.

The fauna of Ulithi falls in the second lot and that is why I hazard a guess that, near the center of each islet there should be a slightly raised coral reef rock.

Dr. Cooke's surmise that Mogmog represents an island of the intermediate type is evidently based on two facts: (1) the number of species of land snails is larger than is known from any other atoll, and (2) not all of these snails have as yet the notoriety of being tourist snails. The unusually large land snail fauna may be due in part to more deliberate and thorough collecting of Mogmog than other atolls have received. Some species have not previously been incriminated as tourist snails, possibly because so little is known about them. Perhaps the richer fauna of Ulithi is only an indication of more frequent commerce than may occur at atolls with smaller snail faunas.

The physical characteristics of Ulithi indicate that it is a typical atoll. Its slight elevation could have been the result of storm action. This is suggested by the small extent and location of the higher areas, as well as by the nature of the material—loose coral rubble—which provided the higher ground. Rubble on the seaward edge of atolls seems to be a common phenomenon, caused by storm action (Hedley, 1896; Wiens, 1962). Wiens noted reports of a severe typhoon in 1906 which "almost destroyed" Ulithi. Even if the elevation of Ulithi is due partly to regional uplift, as is probably the case at Fais, the land height at Ulithi would seem to be too slight to escape the ravages of complete but temporary submersion caused by the Pacific typhoons.

Some of the snails of Mogmog are widely distributed in the Pacific and beyond, and have long been recognized as tourist snails. But of the rest, it is significant that the other localities from which they are known, the Palau Islands,

Guam, and Japan, are all centers with which the Micronesians and Japanese had intensive commerce. The frequent devastation which many atolls including Ulithi experience in typhoons suggests that such atolls may have their land snail faunas periodically much reduced if not obliterated. If we may assume that this happened on Mogmog in 1906, then it follows that all the species of snails found in 1945 arrived between those dates.

Recently I proposed several hypotheses as criteria which may be useful for recognizing exogenous nonmarine mollusca of a given fauna (Harry, 1964). These criteria were derived from my experience with the nonmarine mollusca in temperate North America, and the freshwater mollusca of the Antilles. To what extent they will suffice in the islands of the Pacific has yet to be determined, but we may review them in regard to the snails of Ulithi.

We can be absolutely certain that a snail is introduced into a given area only if it is known that the species was not present in the fauna prior to a certain date, and by having first hand knowledge of the time and method of its introduction. Unfortunately, such information is rarely available. In the Pacific islands, *Achatina fulica* is almost the only example. It is notable that this snail is not known as yet from any atoll, although it lives on the coastal area of some high islands, such as Saipan, where I collected it in 1944. In most cases, circumstantial evidence must be relied on to evaluate a given species as being exogenous.

Most tourist snails have a wide geographic distribution. In the case of the present fauna, all of the species are known to occur on at least one other island, and for some a very extensive range has already been recorded. There is more of such data for the pulmonates than for the prosobranchs, because the prosobranchs have received much less systematic study. All but the *Pythia* and the slug (Vaginulidae) are small in size, and this might have the double advantage of allowing them to be easily concealed and transported both as eggs and as adults. It is a singular fact that of nonmarine mollusca, at least, the tourist species of very largest size are nearly always introduced deliberately, and

usually for food (some Helicidae, *Achatina fulica*, Ampullariidae; see Harry, 1964). But snails of intermediate size, as *Rumina*, *Bradybaena*, some Lymnaeidae, and perhaps *Pythia* and the slug of the Ulithi snails, are to be grouped with the microfauna, since they are only introduced by man accidentally into new areas. Pilsbry (1900) has made the interesting observation that, although regions outside the Pacific area have contributed terrestrial snails as tourists to the Pacific islands (e.g., *Gulella* and *Lamellaxis* of the Ulithi list), those islands have in turn provided no member to the list of tourist snails of other parts of the world. This statement is valid only if we speak of the Indo-Pacific islands rather than merely the Pacific islands *s.s.* Nevertheless, the accidental dissemination of land snails by man within the Pacific area is probably greater than has been previously recognized.

Tourist snails tend to remain in an environment highly modified by man, and do not, through their own natural ability, invade the more natural surrounding areas. This principle is probably as valid for introduced snails as it is for other introduced organisms (Bates, 1956: 788). Thus, man not only is the agent of introduction, but also is responsible for maintaining the environment which allows them to become established in their new locality. At least the biotic environment of atolls such as Ulithi, which are under coconut cultivation, are man-effected situations. Much more ecological work needs to be done on atoll snails to investigate the second part of this hypothesis. Probably there are ecological divisions to be recognized among different atolls, even though superficially their biotas appear very much the same.

There are relatively few species of tourist snails (generally so recognized) which are common to the several low and intermediate islands which have been most intensively studied: of the 17 snails found on Ulithi, only 1 species is recorded among the 22 of Makatea (C. M. Cooke, 1934), only 2 occur among the 11 on Rongelap (Reigle, 1964), and only 2 occur among the 11 on Funafuti (Hedley, 1899). None of the islands cited has more than a few species in common. This may be due in part to diverse patterns of human movement among

these islands. It is equally probable that it indicates ecological diversity.

Tourist snails often have no close relative native to the area in which they are introduced. This rule may have frequent exceptions (Harry, 1964). Among the present fauna of Ulithi there is no single species which is certainly a native, i.e., which has evolved on that island. Thus we can not apply this criterion here. There are nearly as many genera and families as there are species on Ulithi. The chief exception is the Omphalotropidae, which contains two or three species of one genus.

Introduced snails often occur in greater abundance in their new home than in the area where they evolved as indigenous snails. Most of the snails reported herein were abundant. But until we know the natural areas in which the species of the present fauna evolved, such comparisons can not be made for them.

SYSTEMATIC ACCOUNT

Because the pulmonates have been relatively well studied, only the more recent monographic literature is cited for each species. Recent works with extensive descriptions and figures are available for a few of the prosobranchs also, but for several it was necessary to describe and figure them anew, since they have received no adequate treatment in the literature. All the records of species from Fais cited below are given on the authority of Dr. C. M. Cooke.

Order PULMONATA

Family ELLOBIIDAE

Pythia scarabaeus (Linné)

Notes on the growth changes in the shell, and other data on this very common species were presented in an earlier paper (Harry, 1951). The confused nomenclature in this genus allows only *ex cathedra* identification of species at present. The possibility that some species might be tourist snails should be kept in mind in further systematic studies of the group.

Family VAGINULIDAE

Several specimens of (apparently) a single

species were collected, but were lost through unsuccessful attempts to maintain them alive. Lacking data on the internal anatomy, we can not provide even a generic identification. Members of this group have been incriminated as tourist snails (H. B. Baker, 1925; Solem, 1959).

Family TORNATELLINIDAE

Lamellidea subcylindrica? Mollendorff

All of the few specimens were given to Dr. Cooke, who noted that his identification was tentative. The species was described and illustrated by Pilsbry and Cooke (1915), and mentioned in Cook and Kondo (1960:183). The latter note that it occurs on several islands of the Marianas.

Family PUPILLIDAE

Nesopupa ponapica Mollendorff

Pilsbry (1920) reported this only from "Caroline Islands, Mpomp, Ponape," but Mollendorff (1900) thought it might be only a subspecies of *N. tantilla* (Gould), which is widely distributed in Polynesia.

Gastrocopta pediculus Shuttleworth

Pilsbry (1918) reported that this species has been found on nearly every inhabited atoll and high island of Polynesia, Micronesia, and Melanesia where small land shells have been sought. He also reported it in Hawaii, the Philippines, and New South Wales, Australia.

Family SUBULINIDAE

Opeas oparanum Pfeiffer

Pilsbry (1907) could recognize only this species and *Lamellaxis gracilis* Hutton from all of Polynesia, where they are known to be widely distributed by commerce. Several other species of this family are known to be widely distributed in the Pacific islands today.

Family ZONITIDAE

Discoconulus sp. (juvenile)

H. B. Baker (1941) recorded only a single species in this genus, in his monograph of the Zonitidae of the Pacific. While all his records

of it are from the Caroline Islands, he thought it was imported from Japan.

Kororia palauensis Semper

This species also occurs on Fais. Baker (1941) gave an account of the anatomy and distribution. He thought this species was distributed by human agency.

Family STREPTAXIDAE

Gulella bicolor Hutton

This species also occurs on Fais. Germain (1921) gave an extensive synonymy and other data on the occurrence of this snail in Mauritius. It is also found in India, Malaya, and several places in the Pacific islands. I collected it in Saipan in 1944 and in Puerto Rico in 1954. The University of Michigan Museum of Zoology has material from Brazil, French Guiana, Barbados, Panama, and elsewhere. It is undoubtedly a tourist snail, found in the same general area where *Opeas* occurs. The fact that it is less abundant and not so widely distributed as the latter may be due to its carnivorous habits.

Order PROSOBRANCHIA

Family HYDROCENIDAE

Hydrocena (*Georissa*) *laevigata* Quadras and Mollendorff

Hydrocena (*Georissa*) *laevigata* Quadras and Mollendorff 1893, Nachr. d.d. Malak. Ges., p. 42. Not figured. Type locality: Mariana Islands. This species was moderately abundant, and it also occurs on Fais.

Shell (Fig. 1) thick, translucent, amber colored. It is dextral, conic-turbinate in shape, with the whorls evenly rounded, subcircular. Specimens of maximum size have an imperforate umbilicus, and about three suture whorls. The initial whorl is smooth but not polished. It is usually separated abruptly from the later whorls by a transverse line, immediately beyond which there are numerous linear spiral grooves. On the apical part of the body whorl these become vague, and they usually do not continue on the later parts of this whorl, where they are replaced by faint incremental lines. The aperture is subcircular, its height being slightly

shorter than the height of the spire. The outer lip is simple. In submature and mature shells there is a thick columello-parietal plate.

The internal partition of the shell is partly resorbed (Fig. 2), leaving a narrow shelf which is apparently a remnant of the partition, and not a secondary structure, such as that of *Pythia* (Harry, 1951). The partition is complete about $\frac{3}{4}$ whorl in from the aperture. The base of the cavity of the penultimate whorl extends downward to form a conical cavity behind the columello-parietal plate.

The operculum (Fig. 3) is flattened, calcareous, semihyaline, smooth internally, and with an apophysis arising from the slightly elevated nuclear area near the base. The apophysis is narrow, elongate, directed obliquely outward in a gentle curve. It consists of two fused pieces, one not extending to the tip, but the line of fusion is vague. The outer surface of the operculum is covered by a thin, polished, horny layer, reflected along the entire labial margin to form a narrow free membrane. The concentric lamination of the calcareous part, poorly defined and centering around a basal nucleus, is visible through the horny layer.

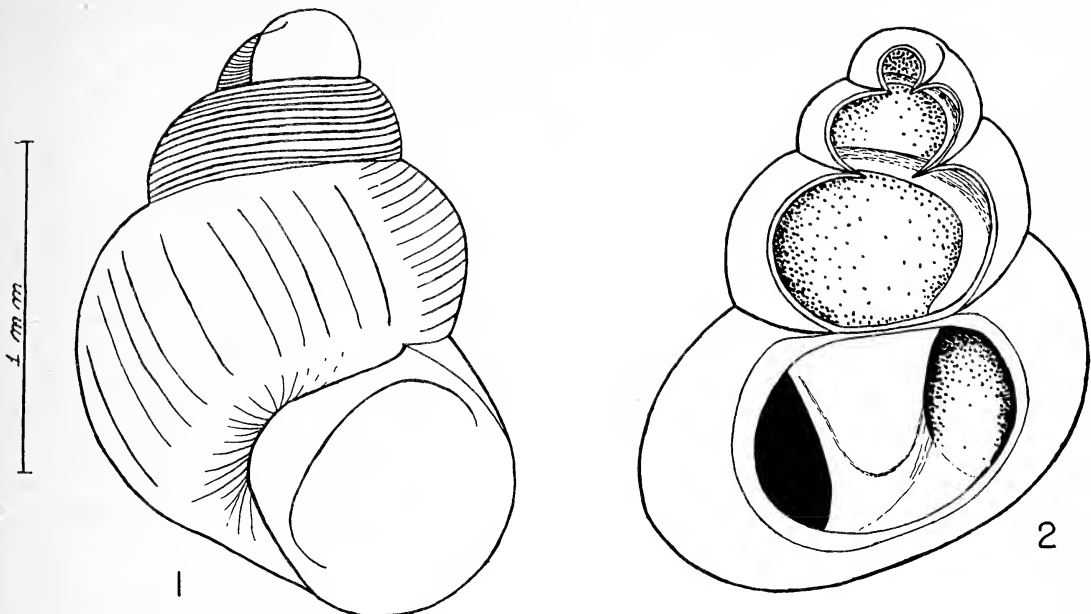
Family PUPINIDAE

Pupina complanata (Pease)

Registoma complanatum Pease 1860, Proc. Zool. Soc. London, p. 440. Not figured. Type locality: "The Island of Ebon, Marshall's group."

Dr. Cooke noted that the Ulithi species was doubtfully present on Fais, and was nearer to *P. complanata* Pease than to *P. berenchleyi* Smith 1891. Clench (1949) has recently monographed this group, providing good descriptions and figures of both species. He recorded *P. complanata* from several localities in the Marshall Islands (type locality) and the Caroline Islands. Mollendorff (1900) cited it as a traveling snail.

The numerous shells from Ulithi present a partial growth series which reveals one of the most remarkable growth patterns to be found in land snails, and one which seems not to have been previously reported. The most juvenile shells (Figs. 4 and 5) have a definitely cyclophorid appearance, with an open umbilicus



FIGS. 1-2. *Hydrocena laevigata*. 2, *Hydrocena laevigata*, opened to show internal shell resorption.

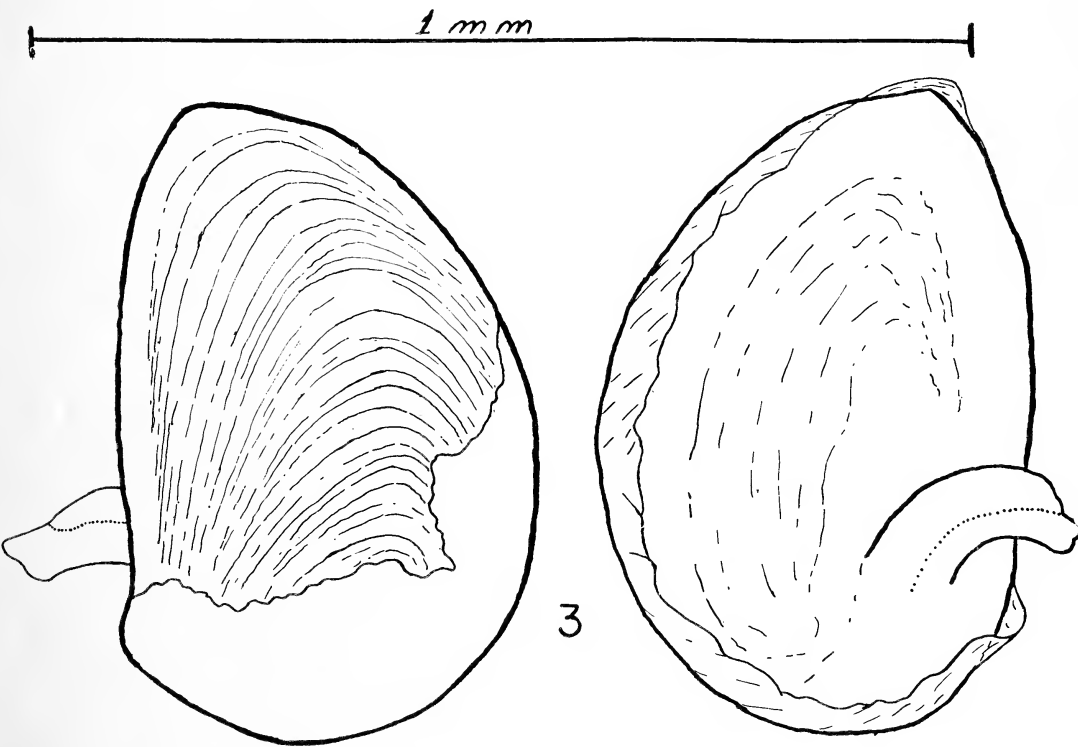
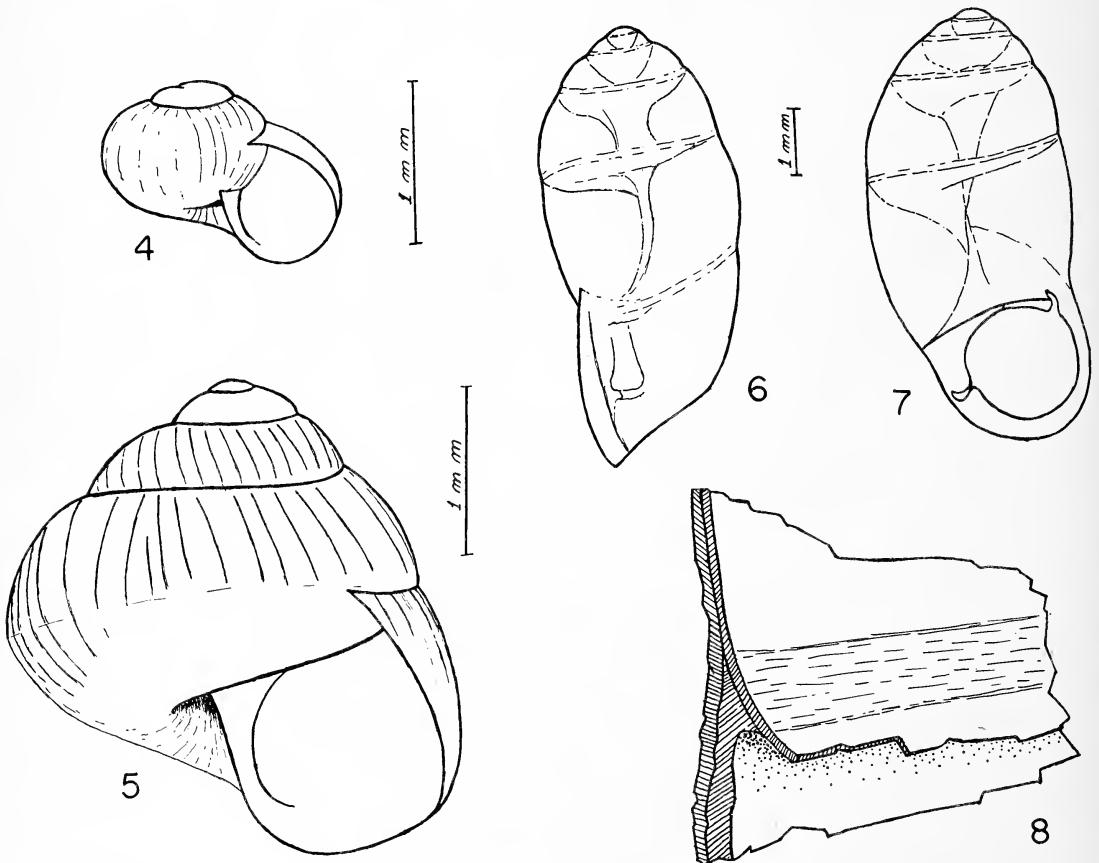


FIG. 3. *Hydrocena laevigata*, operculum.

and prominent transverse sculpture of indented lines. The texture is smooth, but very dull compared with the high polish of mature shells. As more whorls are added the umbilicus gradually closes, and one side of the shell becomes flattened. The plane of the aperture ultimately coincides with the peripheral flattening of the shell. These two features, the closing of the umbilicus and peripheral flattening of the shell, are as much a hallmark of determinate growth as the terminal elaboration of the aperture, which is also present in this genus. Figures 6 and 7 were drawn from specimens in transmitted light, revealing the internal structure of the mature shell. After all the whorls of the shell have been formed, the whole of the outer surface of the shell is covered with a thin, colorless, polished, and glassy layer of shell material,

so that not only the sculpturing of the early whorls, but also the sutures, are obliterated. Figure 8 shows a fragment of a mature shell with the hyaline secondary layer obliterating the suture.

The animal of the Ulithi species was not observed, but several mature, preserved specimens of *P. (Kanapa) brazieri* Crosse, from unknown locality, were studied. These had the mantle margin thin, flush with the lip of the shell, and without papillae or other appendages. The cephalopodal mass was typical of a cyclophorid, with no appendages which might have been reflected over the shell. Exactly how this hyaline layer is formed must await study of the live animal. It seems to be a generic or family characteristic, developed independently in such groups as the Cypraeidae.



FIGS. 4-8. *Pupina complanata*: 4 and 5, juveniles. 6 and 7, two views of the same shell as seen in transmitted light, to show internal structure. 8, a fragment of a mature shell, showing the relation of the hyaline layer to the shell's structure.

Family DIPLOMMATINIDAE

Palaina ovatula Mollendorff

Palaina ovatula Mollendorff 1897, Nachr. d.d. Malak. Ges. 29:42. Not figured. Type locality: Ponape, Caroline Islands.

Dr. Cooke identified this merely to genus, but noted that the same species occurs on Fais. The Bryant Walker Collection at the University of Michigan contains specimens from Ponape which agree closely with the shells from Mogmog, except that they are slightly more ovate. The 38 shells from Mogmog examined are rather uniform in size, form and sculpture. All were slightly weathered, being light grey or dull white, and semiopaque by transmitted light. None contained the operculum or animal.

Shell (Fig. 9) sinistral, ovate-cylindrical, rimate-umbilicate, with $3\frac{3}{4}$ suture whorls. The apex is obtuse, depressed. The whorls are evenly rounded, though somewhat distorted, the later whorls of the spire being slightly flattened. The plane thus produced coincides with the apertural plane. The aperture is subcircular, strongly bilabiate by a heavy, multilamellate costa just before the slightly reflected outer lip. The parietal lip is entirely adnate to the body whorl, and encroaches slightly on it. The latter character is somewhat variable. The aperture has no teeth or lamellae. The initial $1\frac{3}{4}$ whorls are smooth but not polished, beyond which gradually appear minute, lamelliform costae, closely spaced. These gradually increase in size for about 1 whorl, after which they maintain uniform size and spacing until the last half of the body whorl, where they become larger and less closely spaced.

Family TRUNCATELLIDAE

Truncatella (Tabetitia) mariannarum Quodras and Mollendorff

Dr. Cooke considered the Mogmog specimens very similar if not identical to specimens from Guam, which is the type locality. It also occurs on Fais. Clench and Turner (1948) have recently given a review of this group, but did not describe or figure this species, which seems not to have been previously figured.

Adult specimens from Mogmog (Figs. 10, 11, and 12) are about uniform in size, of 9 mm

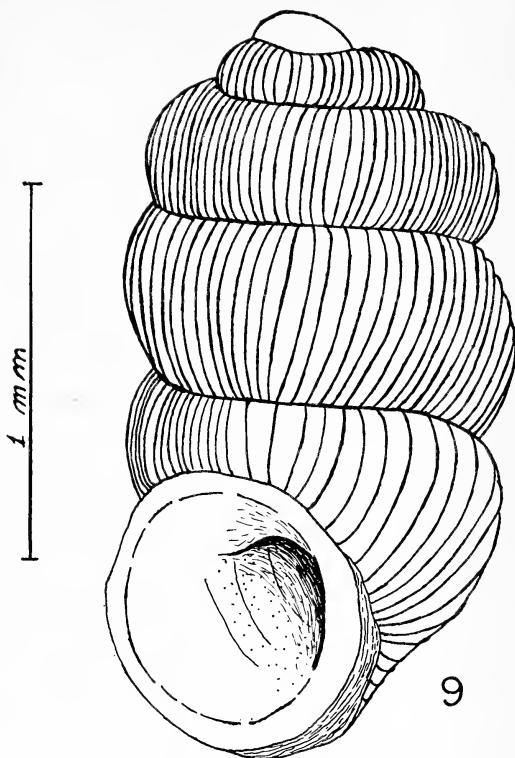
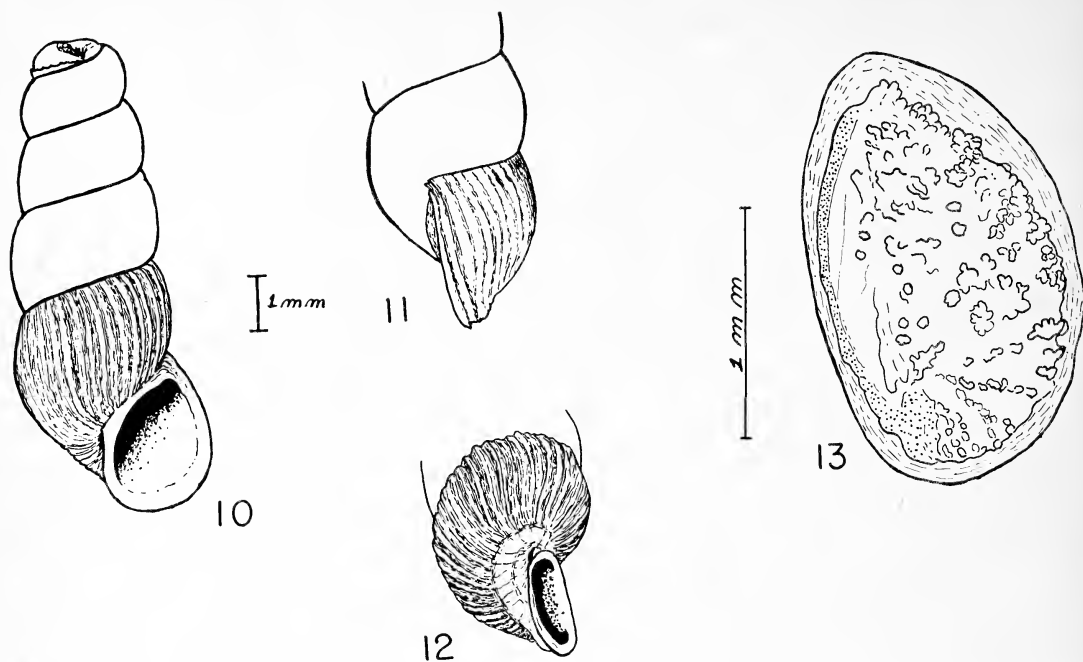


FIG. 9. *Palaina ovatula*.

altitude, decollate, and of about $3\frac{3}{4}$ (suture) whorls. The fine costae number about 40, or slightly less, to the body whorl. On the body whorl there is a moderately vague, linear constriction paralleling the suture a short distance below it. Above this constricting line the costae have a more distinct bladelike aspect than below. The constriction is less prominent on the last fourth of the body whorl and on the whorls of the spire. The base is imperforate, with a basal ridge moderately developed on the last half of the body whorl. Aperture symmetrically ovoid, scarcely expanded, unilabiate, the costae in even size-series before the lip, with none enlarged. Parietal lip moderately thickened, but entirely adnate to the body whorl. The costae do not extend over the basal ridge.

Apex of $1\frac{1}{4}$ whorls, minutely and uniformly costate transversely, with an abrupt transition to the grosser costae of the later shell. Costae of early predecollate shell more acute than those of postdecollate whorls. The color is uniform chestnut brown.



FIGS. 10-13. *Truncatella mariannarum*. 10, 11, and 12, sculpture is shown on body whorl only. 13, *Truncatella mariannarum*, operculum.

Operculum (Fig. 13) with external calcareous plate of moderate thickness, showing vague arcuate-radiate grooving which is more evident toward the periphery. The calcareous plate has a waxy texture. It does not extend to the edge of the operculum.

This species is about the same size and shape as *T. guerinii* A and J.B. Villa 1841, which I have collected on Manus (Admiralty Islands) and Peleliu (Palau Islands). The major difference seems to be that *T. guerinii* has larger costae, which are more sharply defined than in *T. mariannarum* Q. and M. 1894. The two species seem readily separable, with no intermediate forms in the several lots which I have examined. Yet their similarity suggests that they are closely related, and that they may be only subspecifically distinct, or perhaps even phenotypic variations of one species. *T. guerinii* is widely distributed in the Indo-Pacific area, as Solem (1959:197) has noted.

Family ASSIMINEIDAE

Assiminea nitida Pease

The few specimens of this species were all

sent to Dr. Cooke. Garrett (1884) gave an extensive synonymy of *A. nitida*, and noted that it is generally distributed throughout southern Polynesia. Abbott (1949) has figured a cotype of this species and given a description (Abbott, 1958), as well as described several new subspecies. As he noted, it is likely that this has its wide distribution, now known to be from east Africa to the eastern Pacific, owing to the agency of "man and birds."

Family OMPHALOTROPIDAE

Omphalotropis granum Pfeiffer

Hydrocena granum Pfeiffer 1854, Proc. Zool. Soc. London, p. 307. Not figured. Type locality: Isle of Pines, Australian Sea.

Omphalotropis submaritima Quadras and Mollendorff 1894, Nachr. d.d. Malak. Ges., p. 33. Not figured. Type locality: Mariana Islands.

Two specimens of this species were found among the remaining lot of *O. fragilis* after I had divided the material with Dr. Cooke. This may be what he designated merely as *Omphalotropis* sp., from unsorted material which I sent him. The above synonymy is proposed tenta-

tively, as I have seen no material which was undoubtedly the type, cotype, or paratype of Pfeiffer's nominal species. However, the Walker Collection at the University of Michigan contained several lots which are apparently of this same species, and which show it occurs in Lifu (Loyalty Islands), the New Hebrides, New Caledonia, and Guam. The following redescription of this species is based on seven cotypes of *O. submaritima* (University of Michigan Museum of Zoology 77604), which is apparently a synonym.

Shell (Fig. 14) dextral, ovate-conic, solid, pellucid, of $4\frac{1}{2}$ suture whorls. The spire is moderately elevated, its profile forming an acute angle, but with the apex blunted. The suture is simple and deeply set, with the plano-convex whorls being arched sharply just below it, giving the spire a stepped profile. Body whorl vaguely, obtusely angled at periphery. The umbilicus is rimate and concealed by the partially reflexed columellar lip. The aperture is ovate-conic, with outer and basal lip simple, straight, and sharp. The umbilicus is circled by a flat carina, of moderate width, which is variable in prominence. It begins above at the parieto-columellar lip junction, and ends at the baso-columellar junction by a slight angulation of the lip. The color of the shell is corneous yellow. There is occasionally a faint, narrow band of white over the peripheral angulation of body whorl. In fresh shells the embryonic and first whorl are sculptured with minute, closely-set spiral lines, visible only at higher magnification. Later whorls are smooth, but not polished. The operculum resembles that of *O. fragilis* (see below).

The size is variable, though generally uniform among shells of a given lot. Occasionally a specimen may be nearly twice the size of the one figured, with, of course, a proportional increase in the number of whorls. The color also is variable, some lots being light brown, or with a brown band above and below the periphery. The name "*Omphalotropis maritima* Montrouzier" seems to be a nude name, which was first printed in Paetel's catalogue. However, it accompanies many of the older museum lots, and may have given rise to the inapt trivial name

applied to this species by Quadras and Molendendorff.

Solem (1959:200) has independently recognized that *O. submaritima* Quadras and Molendendorff is a junior synonym of *O. granum* Pfeiffer, and he has also included "*O. maritima* Montrouzier" with them parenthetically. The *O. setocincta* Ancey 1890 which he recognized from the New Hebrides and figured (Solem, 1959: Plate 27, figs. 8, 9) is so close to the specimens from Ulithi and to the cotype of *O. submaritima* which I have drawn (Fig. 14) as to suggest that they represent the same species.

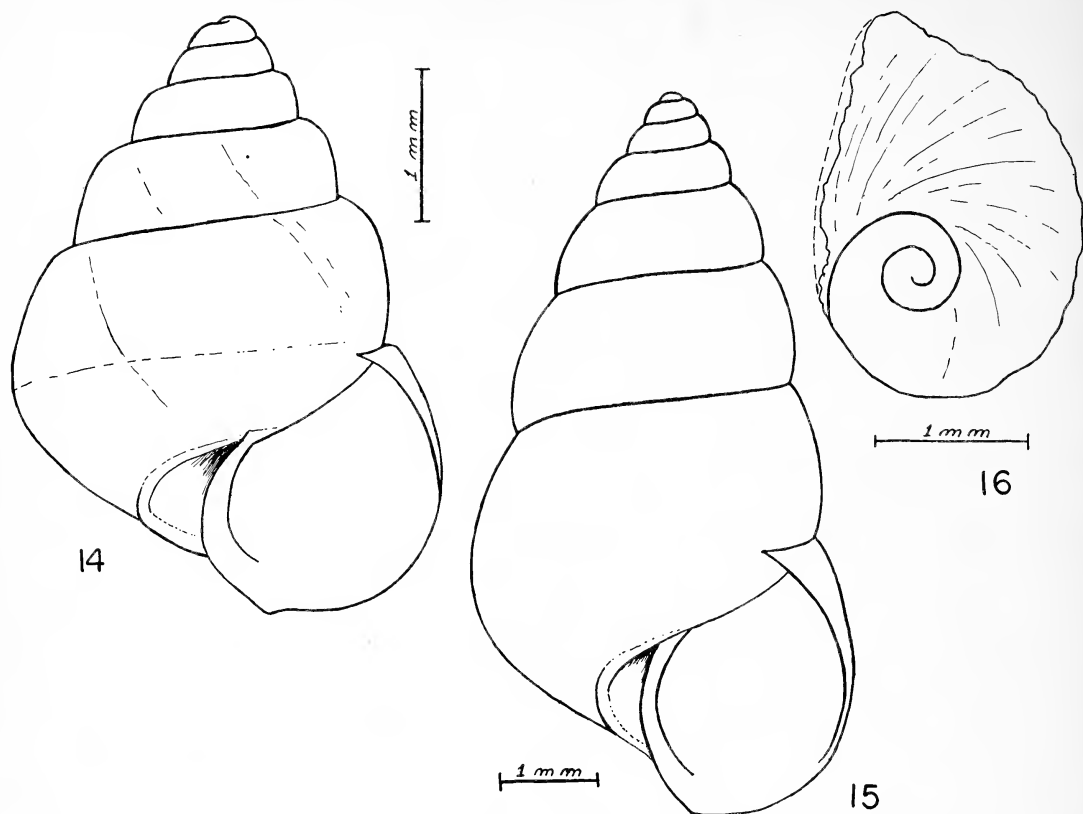
Omphalotropis fragilis Pease

Hydrocena fragilis Pease 1860, Proc. Zool. Soc. London, p. 439. Not figured. Type locality: Ebon, Marshall Islands.

Dr. Cooke noted that this species also occurs on Fais.

The shell (Fig. 15) is dextral, thin, translucent, turbinate, rimate-umbilicate. The apex is bluntly rounded, with the first two postapical whorls somewhat more convex than later whorls, which are only slightly, but evenly, rounded. The suture is prominently impressed. Periphery of juvenile shells (5 suture whorls) distinctly angled, and usually with a vague, linear callus, but this disappears on shells of maximum size ($6\frac{1}{4}$ suture whorls) which show scarcely any angulation of the periphery. The base is slightly inflated, with a carina circumscribing the small umbilicus, typical of the genus. Aperture ovate, with the columellar lip slightly reflected, and with an angle at the end of the omphalotropid circumumbilical callus, at the junction of the basal and columellar lips. Apical whorls are smooth, without sculpture. There is no sharp dividing line between apex and later whorls. The silky texture of later whorls is caused by numerous, minute, vague, spiral lines. These are evenly distributed from suture to umbilicus, but variable in their presence in different shells.

Although the shell shape is remarkably constant, the color is extremely variable. Shells may be uniformly colored, either very light yellow or dark reddish-brown. Several spiral bands of dark brown may be present, and may be variable in width and number. Transverse bands of dark maroon, irregular and discontinuous, may occur



FIGS. 14-16. *Omphalotropis*. 14, *Omphalotropis submaritima* = (*granum*), cotype, from Guam (University of Michigan Museum Zoology No. 77604). 15, *Omphalotropis fragilis*. 16, *Omphalotropis fragilis*, operculum.

alone or in combination with the spiral bands.

Shells of maximum size have $6\frac{1}{4}$ suture whorls and measure 6.0 mm high, and 3.3 mm greater diameter. The operculum (Fig. 16) is corneous, light brown, and paucispiral.

Possibly the *Omphalotropis zebriolata* Mouson cited by Hedley (1899:417) from Funafuti and many other Pacific islands is identical or closely related, but I have had no access to material which would settle this problem.

Omphalotropis suturalis Quadras and Mollendorff

Omphalotropis suturalis Quadras and Mollendorff 1894, Nachr. d.d. Malak. Ges. 26: 22. Not figured. Type locality: Mariana Islands.

The few specimens were all sent to Dr. Cooke, who noted that he could not separate the Ulithi specimens from those of Guam.

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Some Aspects of the Behaviour of the Soldier Crab, *Mictyris longicarpus*

ANN M. CAMERON¹

THE CRAB, *Mictyris longicarpus* Latreille 1806, belongs to the brachyuran family Mictyridae Dana 1856. According to McNeill (1926) the species ranges northward from southern New South Wales and from Perth, Western Australia, to New Caledonia in the east, to Singapore in the north, and to the Bay of Bengal in the west.

In Australia *Mictyris* is known as the "soldier crab." This appellation is appropriate in view of the habits of the genus. Immense numbers of *M. longicarpus* (Figs. 1 and 2) congregate in dense masses and wander over tidal flats in apparent formation. Their activities exert a particular fascination not only because of these huge "armies," but also because soldier crabs walk forward and not sideways, as do most crabs. Several authors have commented on the habit of *Mictyris* of wandering in armies (McNeill, 1926; Lazarus, 1945; Balss, 1955-56; Altevogt, 1957; Schöne, 1961; Stephenson, 1961). However, little is known of the organisation of this behaviour and I decided to study *M. longicarpus* with a view to describing it. Because of the immediate flight and burrowing reactions of soldier crabs to the disturbing influence of observers, the pattern of behaviour to be described has been previously overlooked.

METHODS

Field observations were made from within a pentagonal plywood hide, 3 ft high, in the sides of which uncovered windows, 11 × 6 inches, were cut. A tripod was used for mounting binoculars and a 16-mm movie camera. On each occasion a place was selected prior to the appearance of the crabs, and observations were made from there for the duration of that particular intertidal period. (Transference of the

hide to another area of the beach after the appearance of the crabs invariably disturbed them, and was attempted only a few times.) Apart from the displacement activity to be described later, the crabs did not appear to be disturbed by the presence of the hide.

Field observations were made at least twice a month, and frequently as often as six times a month, throughout 1961 and the first half of 1962. Most of the observations were made at Dunwich, Stradbroke Island and at the mouth of the Pine River (Fig. 3). Localities at which additional observations were made are shown in Figure 3 also.

No period of observation at any one locality was of sufficient duration to allow study of any lunar rhythm in soldier crab activity.

HABITAT

Although Lazarus (1945) stated that *Mictyris* is found "where the mixture of silt and sand is fairly coarse and free from matting mangrove roots," it was observed that the crabs burrow in a wide range of substratum types from silty sand to shell grit. However, material collected from the top 2 inches of a typical *M. longicarpus* habitat at Dunwich (Fig. 3) contained 95-98% sand of particle size 1.96-0.05 mm (F. C. Vohra, personal communication). The method of analysis consisted of removal of gravel, calcium carbonate, and organic matter, followed by sieving the coarse fraction and sedimentation of the fine fraction.

Stephenson (1961) has described the habitat of *M. longicarpus* at Dunwich, where the crabs are found in both clean sand and in areas of muddy sand covered with the eel grass, *Zostera capricorni*. The beach at Dunwich is very wide and flat. No *Zostera* grew in the study area at Pine River, and the beach there has extensive drainage channels in some parts and secondary sand bars in others.

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BEHAVIOUR

Numerous environmental factors such as tide, temperature, solar radiation, precipitation, and wind are generally considered to influence the activities of mobile intertidal animals and of shore crabs in particular (Crane, 1958). Soldier crabs are usually active for several hours before and after low water, although they are more active on warm sunny days than in cold overcast conditions. They were observed to be active at night, but their nocturnal behaviour was not studied. In daylight hours, cessation of activity and retreat below the surface were frequently observed in response to apparently unfavourable conditions, such as the onset of rain. Such periods of retreat ranged from a few minutes to the remainder of an intertidal period.

A pattern of activities is followed by undisturbed populations of *M. longicarpus* during the intertidal period. This pattern will be described as a series of phases of activity, each of which merges with the one following but is nevertheless generally well defined. Variations in the sequence and in the duration of each phase occur, and the pattern may be interrupted or terminated by unfavourable environmental conditions.

1. Subterranean Phase

Activities performed below the surface were not studied, but indications of subterranean ac-



FIG. 1. Adult male *M. longicarpus*. (Photograph by S. Breeden.)

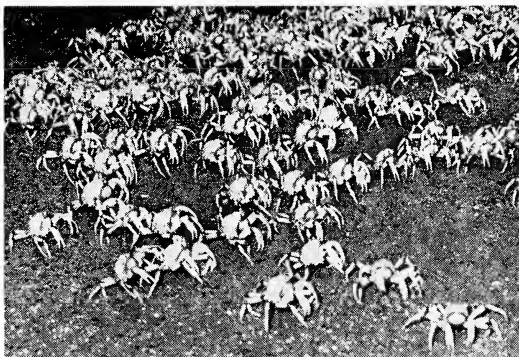


FIG. 2. Section of an army of *M. longicarpus*. (Photograph by B. Morgan.)

tivity become obvious some time before the crabs make their appearance. On the surface of the previously smooth sand small hummocks appear and increase in dimensions (Fig. 4). These hummocks are always made prior to the crabs' emergence but their formation does not necessarily imply that the crabs will emerge. Hummock building lasts from 10–30 minutes. Just prior to the second phase of activity the summits of the hummocks are broken open (Fig. 5).

2. Emergence Phase

A population may emerge in less than five minutes, or the period may be protracted for as long as one hour. Generally adults emerge before the juveniles. Takahasi's (1935) statement that "*Mictyris* never comes out to the surface" is inexplicable. It was ascertained by digging that many individuals remain beneath the surface for an entire intertidal period. Thus, the emerged population does not represent the total population of the area. Further, the proportion of the population which does emerge varies on subsequent days. At any locality the emerged population may be nearly all adult males on one day, and a mixture of all sizes and both sexes on the following day. McNeill (1926) thought that female *M. longicarpus* do not congregate on the surface to the same extent as do the males. This was verified in the present study.

Upon reaching the surface individuals perform a routine of body care, in which they remove adhering sand grains from the eyes, mouthparts, and carapace. They clean the eye-

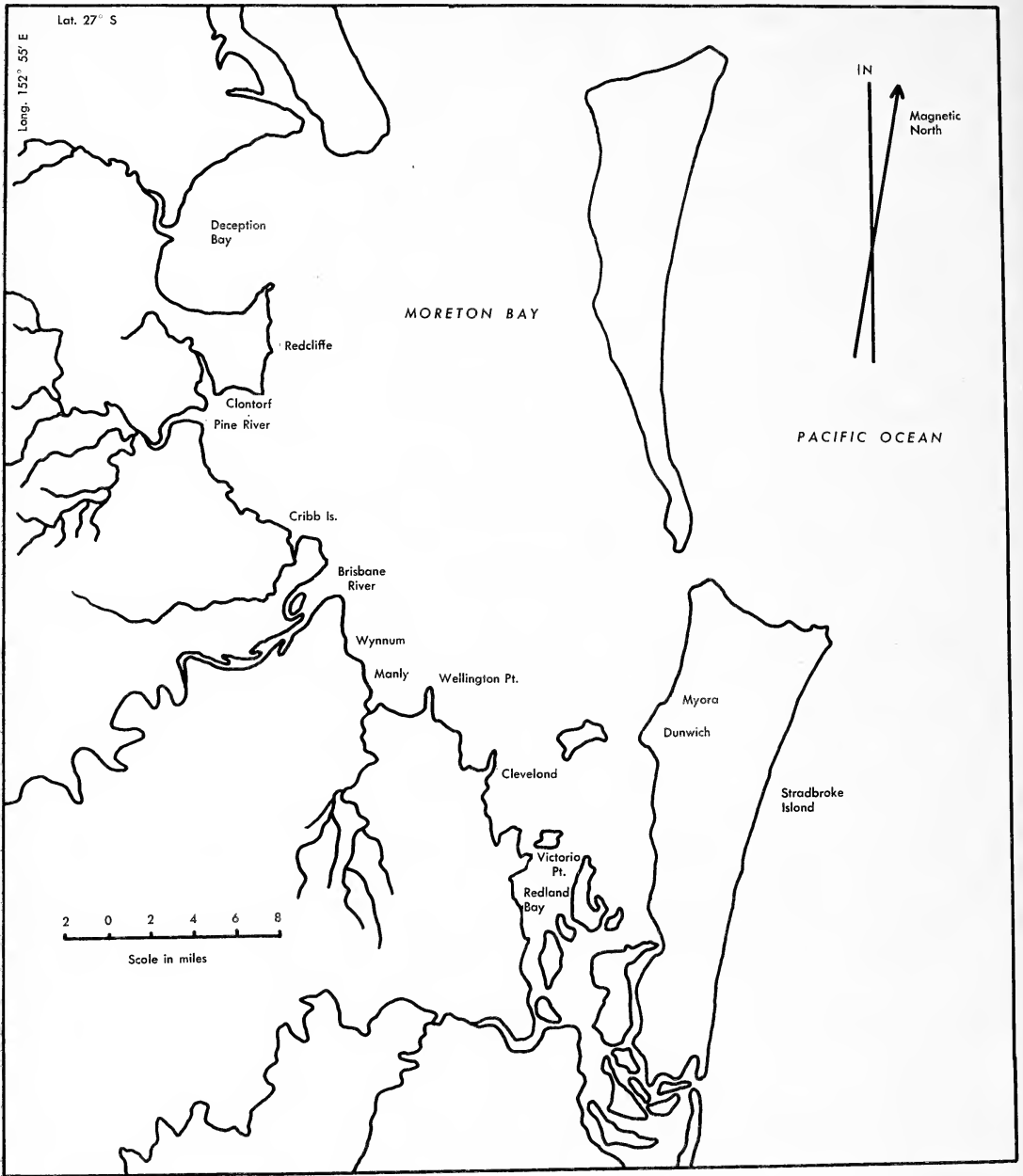


FIG. 3. Map of Moreton Bay, Queensland, showing localities at which field observations were made.

stalks and mouthparts by vigorously rubbing the chelae over these regions. Cleansing is facilitated by vibratory movements of the third maxillipeds and by alternate raising and lowering of the eyestalks. Sand on the carapace is removed as a result of a "back-flip" manoeuvre. This is essentially a half somersault and is executed in

less than a second. The crab falls backwards, lies with the carapace on the substratum, and then flips back to the normal resting position.

3. Preliminary Feeding Phase

Subsequent to emergence the crabs feed and walk alternately, the feeding rate being much

slower than that of normal feeding (phase 5). This phase occupies 10–15 minutes. Those crabs which are first to emerge do not immediately feed in this slow fashion, but run about, stop, remain motionless, run further, and so only gradually begin to feed. The slightest disturbance at this stage, such as the flight of a bird overhead, results in their immediate retreat below the surface, from where they emerge again after about 3 minutes.

4. *Trekking Phase*

Within 15 minutes of emergence the crabs simultaneously begin walking toward the water. This spectacular migration is termed the "trek." Usually the movement is down the beach, but if surface water is present in channels or run-offs the direction of the trek is across the beach toward these channels. Walking of individuals is interrupted by frequent short stops to feed, but the movement of the population as a whole does not stop until the water is reached. Trekking occupies 15 minutes at the most, and is nearly always performed in a virtually straight line from the area of emergence.

There is no cohesion among the individuals during the trek. Each crab makes its own way down the beach and the population appears dispersed at random. Generally, a distance of about 18 inches separates the individuals, which reflects the fact that they have emerged in proximity, and have proceeded at the same rate. Juveniles do not take part in the trek proper. They usually move about 50 yards in the general direction taken by the adults, and then wander about feeding at this level of the beach.

5. *Feeding Phase*

When they have trekked to areas which apparently are suitably moist, the crabs increase their rate of feeding until it is extremely rapid. They progress as they feed, the direction of movement being more or less along the beach parallel to the water. Frequently, they transverse the *Zostera*-covered areas on beaches where the grass occurs.

McNeill (1926) and Lazarus (1945) have described the mechanics of soldier crab feeding. Portions of the substratum are lifted to the buccal cavity and are sampled by the mouthparts. I observed that material unsuitable for ingestion

accumulates at the bases of the third maxillipeds, and is discarded in the form of pellets (Fig. 6) which either drop off, or are wiped away from the ventral surface of the body by a lateral movement of one of the chelae. A similar deposition of discarded material is performed by *Uca* spp. (Miller, 1961) and *Dotilla micityroides* (Tweedie, 1950). Feeding pellets deposited by crabs in the van are generally left undisturbed by following crabs.

As the feeding phase progresses, the initial rapid rates of walking and of deposition of pellets slow down. Aggregation into groups of about 100 crabs takes place, and the individuals continue to feed, although the groups dissolve and reform continuously. After about ½ hr, the formation of larger aggregations, called armies, takes place. Such groups are distinguished from the former feeding groups in that the individuals of armies tend to remain in company, whereas previously they lacked this cohesion. Feeding continues. The armies increase in size by the addition of recruits either singly or in groups, until aggregations of many hundreds are formed. The duration of the feeding phase is variable. Usually it lasts for about 1 hr, but often can be for as long as 2½ hr. With diminution of the feeding rate, the armies begin to move over the shore, frequently remaining in puddles and run-offs and performing no visible activity.

Examination of the gut contents of soldier crabs was made by dissecting the alimentary canal under the microscope, and staining the organic matter present with Toluidine Blue and Methylene Blue. Almost all the material in the gut was organic debris. Some very fine silt was present, but there were no sand grains in the cardia as reported by Lazarus (1945). Diatoms occurred in all, though not as a major constituent of the contents, and one specimen contained gastropod eggs and a nematode. These data agree with those of Lazarus (1945) who stated that the food of *Mictyris* is "organic fragments and minute organisms" extracted from the sand. However, she remarked that, although "the mouthparts must discard much of this useless sand the gut is usually full of it either in its original state in the cardia or ground into a finer consistency in the intestine." Since soldier

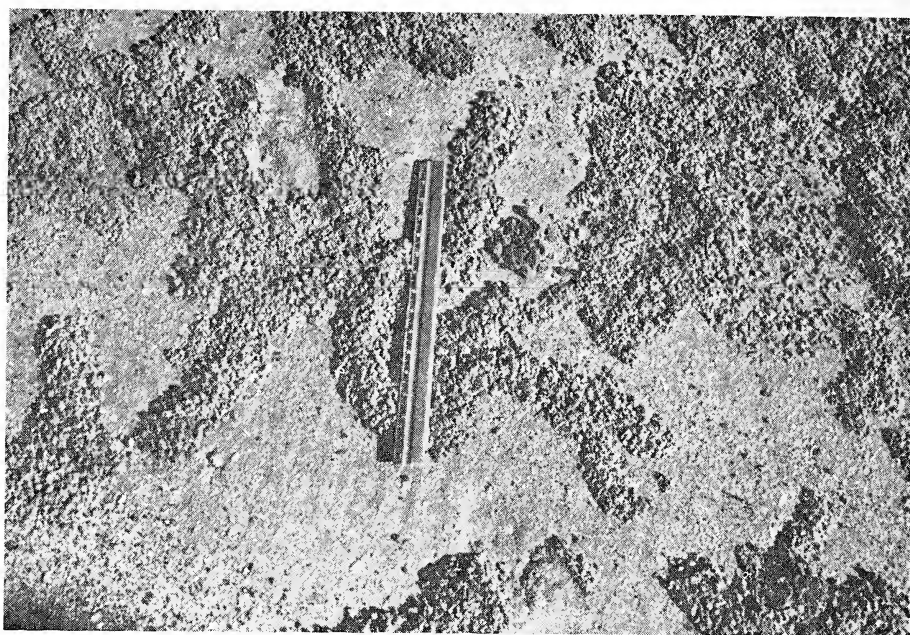


FIG. 4. Hummocks made prior to the emergence of the crabs. (The ruler is 15 inches long.)

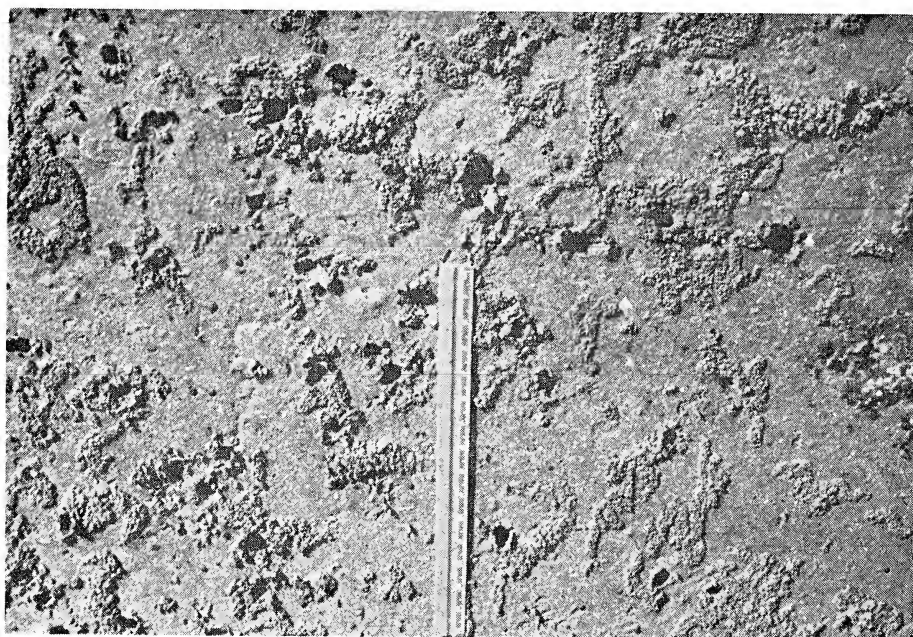


FIG. 5. Holes opened by emergence of the crabs. (The ruler is 15 inches long.)

crabs may feed for periods of the order of 2 hr, it would seem impossible for the gut to accommodate a continuous intake of sand for this length of time. The fact that they habitually

feed for such extended periods favours the explanation that they need to sample a large volume of sand, and that they efficiently select from this the small fraction suitable for inges-

tion. Furthermore, the faeces of the animals are devoid of sand grains.

In discussing the feeding mechanism of *Uca*, Miller (1961) remarks that "the thoroughness with which the crabs are able to sort food material from the mineral fraction of the substratum corresponds to the availability of the food material." He showed that the sandy beach-inhabiting *U. pugilator* ingests a minimal amount of sand, whereas for the marsh-inhabiting *U. pugnax* "food is more readily available because the silt with which it is generally associated is of sufficiently fine texture to be ingested." Furthermore, in those ocypodid crabs which possess them, the spoon-tipped setae of the mouthparts are present in greater numbers and exhibit more elaborate spooning in species inhabiting sandy substrata than in species of muddy environments (Crane, 1941, 1943; Altevogt, 1957; Miller, 1961). *Mictyris longicarpus* possesses large numbers of densely packed spooned setae. They are present on the inner surface of the third maxillipeds, the outer and inner surfaces of the second maxillipeds, the basipodite of the first maxillipeds, and the outer surface of the endite of the coxopodite of the first maxillipeds. There are four types of

spooned seta, which are shown in Figure 7.

6. Army Wandering Phase

Soldier crab armies present a spectacular sight. They may cover vast areas of the beach and their tightly packed masses create a rustling noise audible at a considerable distance. The army wandering phase begins with the cessation of feeding. Sometimes the transition is sudden but usually it is gradual. Armies are generally composed of similarly sized individuals, usually adult males. Only rarely do females wander in armies, though mixed armies occur. In mixed armies, the largest crabs progress in the vanguard, probably because they walk faster than do the smaller ones. In no sense does any section of an aggregation lead the rest. The advancing front changes continuously, and the crabs often walk over each other, two and three deep, in the general scramble. Crowding may be even worse than this, especially when the advancing front reaches standing water and stops. Armies cover great distances during this phase. They commonly walk as far as 500 yards, the rate of progression being about 10 yards per minute. Army wandering occupies from 30 minutes to 2 hr. When emerged females are present but have not joined armies, their feeding activities



FIG. 6. Feeding pellets deposited by soldier crabs. (The ruler is 15 inches long.)

(phase 5) merge with the return phase (7) described below. Juveniles do not participate in army wandering.

7. Return Phase

The return phase begins when the armies cease to wander about the beach in a seemingly undirected fashion, and orient their progression in the direction of the upper levels of the shore. As they proceed, individuals tend to dissociate themselves from their fellows so that the armies lose their cohesion. The crabs continue walking until they reach the level of the beach at which they emerged. This return may be protracted for as long as $1\frac{1}{2}$ hr, but it may be as short as 15 minutes.

8. Aggressive Wandering Phase

On completion of the return phase, the crabs dig holes in typical corkscrew fashion (McNeill, 1926). Although McNeill believed that these burrowing actions "are probably unique among the Decapoda," Tweedie (1950) has since noted that *Dotilla mictyroides* employs a similar method. Soldier crabs do not remain in these newly dug holes but re-emerge, dig more holes, abandon these in turn, and continue thus for the duration of the phase. At the same time they respond to encounters with one another. Threat displays between pairs of adult males result from these encounters. In each case, one of the pair of crabs involved was temporarily associated with a hole. Females were not observed to participate in such displays. Four types of encounter were observed: (i) walking over an occupied hole, followed by emergence of the occupant and a threat display between him and the intruder; (ii) physical collision of two crabs in the vicinity of a hole, followed by a threat display; (iii) threat display by an occupant at the entrance of a hole, to which another male in the vicinity responded with a threat display; (iv) intrusion by a male into an occupied hole, or digging by a male so close to an occupied hole that its occupant emerged, followed again by a threat display.

Soldier crab threat display is performed as follows: Rival males meet. Each raises the anterior legs off the substratum so that he is balanced on the third and fourth pairs of walking legs, or even on the most posterior pair alone.

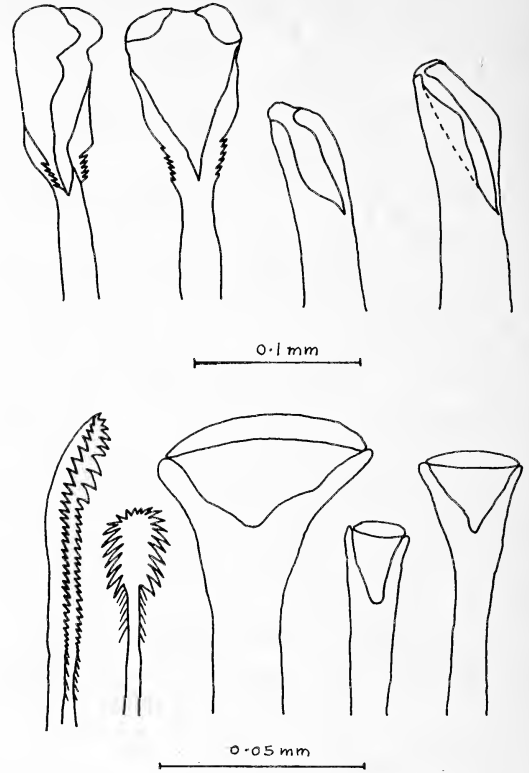


FIG. 7. Camera lucida drawings of the four types of spoon-tipped seta on the mouthparts of *M. longicarpus*.

Those walking legs thus freed are extended laterally, as are the chelipeds. Attainment of the posture of maximum threat occurs when the plane of the thoracic sterna is vertical. Thus, the ventral surfaces of the crabs are brought into proximity. However, they do not touch, and no pushing occurs. The eventual winner may remain poised in the position of maximum threat for up to a second after the loser has fallen away. Throughout the encounter the free walking legs are vibrated rapidly, and the chelipeds are gradually raised vertically from their position of horizontal extension. Immediately after the display the winner exhibits the following characteristics: (i) maximum vertical extension of the chelipeds, (ii) maximum extension of the free walking legs, (iii) maximum extension of the legs on which he is balanced, (iv) maintenance of the eyestalks in the raised position, and (v) maintenance of position with respect to the hole.

The loser is characterized by: (i) lowering of the chelipeds, (ii) flexion of the free walking legs, (iii) flexion of the legs on which he is balanced and subsequent dropping to the substratum, (iv) lowering of the eyestalks, (v) submissive posture in front of the still threatening winner, and (vi) retreat from the vicinity of the hole.

Although the winner may remain in the vicinity of the hole for a few seconds, he generally moves away shortly after the loser has departed.

A stopwatch was used to time 84 threat displays. The longest encounter lasted for 30 sec and the shortest for one sec. From the data collected, the significance of occupancy of a hole, and of disparity in the sizes of the participants were estimated. Occupancy was indicated by a crab's position either within a hole or in its immediate vicinity. Size was subjectively determined with categories of "bigger," "smaller," and "apparently equal." The error in allotting a pair of individuals to the last category may be considerable, but not so great as to obscure the general picture revealed by the data. That this error in categorisation was consistent is indicated by the coefficients of variability calculated for data of threat displays between apparently equal-sized crabs on the one hand, and between unequal-sized crabs on the other. These are 57% and 54%, respectively.

Of 42 threat displays between unequal-sized crabs, 38 were won by the larger of the pair. Less than 10% of these encounters were won by individuals perceptibly smaller than their opponents. Of 40 threat displays between apparently equal-sized crabs, 35 were won by the occupant of the hole. Clearly, occupancy is an advantage.

The mean time of threat displays between apparently equal-sized crabs (9.8 sec) was compared with that of threat displays between unequal-sized crabs (7.8 sec) by use of a "t" test. The means are probably significantly different (p between 0.05 and 0.1), indicating that disparity in size of the participants shortens the time of threat display, compared with that elapsing during threat display between apparently equal-sized crabs.

Only four instances of threat display were observed in which neither participant was in

the vicinity of a hole. In each case the larger individual won.

A considerable degree of social facilitation was evident in dense populations of soldier crabs during this aggressive wandering phase. On many occasions threat displays between pairs of crabs were joined by a third, fourth, and even a fifth individual. Each individual participating in these multiple displays assumed the typical threatening posture as far as the crowded space occupied by the several crabs allowed.

Threat display occurred throughout the year. Breeding also occurred throughout the year. In no month from February 1961 to October 1962 were ovigerous females absent in the populations studied.

The aggressive wandering phase may continue for as long as $1\frac{1}{2}$ hr but generally occupies about half that time. Threat displays are frequent throughout the phase. As many as 12 such displays were observed simultaneously in an area 20 ft square. Aggressive wandering diminishes as the individuals remain in holes instead of re-emerging, and the whole population gradually disappears beneath the surface.

For each of these phases of activity during the intertidal period, the approximate duration has been given. It is emphasised that these times are highly variable, and that the entire sequence is not always completed. Although the initiation of each phase is generally synchronised for all the individuals of the emerged population, occasions were noted when feeding, army wandering, and returning were being performed simultaneously in different areas of a large beach.

REACTIONS TO OTHER ORGANISMS

During this study seven species were observed to prey on *M. longicarpus*. They are *Threskiornis spinicollis* (Jameson), the straw-necked ibis; *Halcyon sordidus* (Gould), the mangrove kingfisher; *Egretta alba* (Linné), the white crane; *Sphaeroides hamiltoni* (Richardson), the toad fish; *Ocypode ceratophthalmus* (Pallas), the ghost crab; *Metopograpsus messor* (Forskål), a grapsid crab; and *Conuber sordida* Swainson, a sand snail. The ghost crab and the sand snail preyed on juvenile soldier

crabs. Toad fish captured adults in run-off channels. *M. messor* seized soldier crabs near a rocky point at Dunwich (W. Stephenson, personal communication). The three birds preyed on adults, usually during the army wandering phase of activity. It is noteworthy that, except for a slight increase in the walking rate of the crabs at the approach of a predator, they exhibited no escape reactions. This contrasts strongly with the behaviour of soldier crabs in the presence of human observers. Their reactions in such circumstances are as follows:

1. Burrowing. On being chased by humans, soldier crabs burrow in typical corkscrew fashion.

2. "Fright reflex." *M. longicarpus* occasionally reacts to the presence of an observer by assuming a "frozen" posture in which the limbs are extended rigidly. The presence of normal predators was never observed to elicit this response, common among brachyurans (Schöne, 1961: 474.)

3. Crouching. A crab in this posture lowers the body to the substratum and folds the flexed legs as closely as possible to the body. The eye-stalks are lowered.

4. Interspecific threat. Occasionally, crabs which were being chased by the observer, raised the chelipeds and ran away from the observer. This ambivalent behaviour is apparently an attempt to flee and to perform a threat display simultaneously.

5. Displacement feeding. Displacement feeding differs from the autochthonous activity in that any material that is raised to the vicinity of the buccal opening is never introduced into it, and consequently no feeding pellets are formed. Two types of displacement feeding occur.

- a. A crab remains stationary, continuously raising and lowering the chelae which may or may not touch the substratum. No material is picked up, and the chelae are not lifted as high vertically as they are in normal feeding.

- b. Displacement feeding of the second type has a much more "nervous" appearance (in the sense in which this term is used by Gordon, 1955). Walking with unusually rapid steps, a crab lowers the chelae and picks up material from the substratum in such quantity and with such lack of normal manipulative dexterity as

to drop it immediately. The chelae continue their upward movement but do not reach the buccal opening. Furthermore, material not conveyed to the mouthparts during normal feeding is picked up in this displacement feeding, for example, small pebbles and pieces of *Zostera* two inches long.

It is evident that these two types of displacement feeding are essentially similar, differing in their degree of disorientation to the environment, rather than in their organisation. Such correlation between intensity of thwarting or conflict and the degree of disorientation of displacement activity is well documented (Armstrong, 1950).

Circumstances eliciting displacement feeding in *M. longicarpus* are:

- (i) Simultaneous activation of the drives to retreat and to stay. Crabs were disturbed by the observer until they retreated, after which the observer remained motionless at a distance of approximately 10 ft. After a few seconds the crabs halted and, while either standing stationary or approaching the position of the observer, began displacement feeding. As they approached, the rate of movement of the chelae increased.

When the observer's hide was placed in such a position that the crabs trekked around or past it, they began displacement feeding as they approached to within about 4 ft. Some individuals spent as long as 3 minutes at a distance of less than 4 ft from the hide, displacement-feeding throughout that interval. Then they made their way past the hide and ceased displacement feeding at about 4 ft from it.

- (ii) Simultaneous activation and thwarting of the escape drive. Soldier crabs were chased until they burrowed. When the excavation was as deep as the body of the crab, the crab was removed from it and placed on the surface beside it. The crab burrowed again, and was again interrupted. After about five repetitions of this interruption, some of the crabs so treated began displacement feeding. Many could not be induced to do so, but assumed the crouching posture described above.

All the instances of displacement activity described above were induced by the presence of the observer or of the hide, or by interference.

No displacement activity was observed in any other circumstances.

DISCUSSION

Several aspects of the behaviour of *M. longicarpus* are of interest. It would appear that the preliminary feeding phase may be regarded as appetitive feeding. Normal feeding does not take place until completion of the trek. The obvious result of trekking is that the crabs move from the upper levels of the beach to the more moist areas. Altevogt (1957) postulated that all ocypodid crabs possessing spooned setae on the mouthparts select nutritive material from the sand by the "flotation" method he observed in *Uca* spp. Water is lost continuously through ingestion, evaporation, and in the discarded pellets. Miller (1961) investigated this topic for several species of *Uca* and concluded that the need for water is reflected by the moist condition of the material from which these crabs prefer to feed. This appears to be the case for *M. longicarpus*. Not only do soldier crabs possess dense spoon-tipped setae, but also they frequently feed in depressions and in run-off channels.

Trekking is most obvious on wide, gently sloping beaches where the crabs may remain on the surface for as long as 4½ hr. Where the beach is narrower and of steeper slope, they do not remain on the surface for such lengths of time, and they generally emerge earlier with respect to the time of low water than do those inhabiting the wider flats. On beaches of unusual configuration, such as those at the mouth of the Pine River, the direction of the trek is determined by the proximity of extensive drainage channels. Moving down the beach would bring them to the elevated sand bars. From the bars to the river the beach slopes in the normal way, and the crabs in this area trek down in the usual fashion.

When feeding has ceased, the army wandering phase takes place. In some respects, the behaviour of soldier crabs in this phase resembles that of *Uca* in the "nonaggressive wandering phase" described by Crane (1958). While it is evident that the aggregations in which feeding takes place subserve coverage of a widely dis-

persed food supply, the presence of the animals on the surface after feeding has ceased is enigmatic. Whatever are the physiological functions performed at this stage, they must be of considerable significance in view of the energy expended in wandering about the beach, and of the danger from predators to which the aggregations are exposed. These phenomenal aggregations, in which the individuals perform no visible activity other than walking, may be an example of epideictic display (Wynne-Edwards, 1962).

Threat display is associated with competition for space, the space being a hole occupied by one crab and intruded into by another. Occupancy of a hole, however temporary, appears to be the manifestation of a poorly developed territoriality, and for this reason the threat display must be considered reproductive fighting. Tinbergen (1952) remarked that displacement activities occur most frequently during boundary disputes. No instance was observed of either of the participants in a threat display subsequently performing displacement activity. This is not unexpected, in view of the transitory nature of soldier crab "territory," which is based on occupancy of a hole and not on construction and maintenance of a permanent burrow.

There are similarities between the intertidal behaviour patterns of *M. longicarpus* and *Uca* spp. (Crane, 1958). The activities of both are organised into a series of phases. There is a temporal separation of feeding, and of other activities. Although there is nothing comparable with the waving display of *Uca* in the behaviour of *M. longicarpus*, the occurrence in the latter of threat display, and its nature, are of interest.

SUMMARY

1. *Mictyris longicarpus* performs a sequence of phases of activity during the intertidal period: subterranean activity, emergence, preliminary feeding, trekking down the beach, feeding, army wandering, return up the beach, aggressive wandering, return to subterranean burrows.

2. Dense, elaborate spoon-tipped setae are present on the mouthparts of *M. longicarpus*.

3. Wandering in armies occurs after feeding has ceased. Adult males comprise the majority

of these aggregations.

4. Threat display occurs between pairs of adult males. Occupancy of a hole, and larger size of a male, are advantageous in such displays.

5. Displacement feeding occurs as a result of conflict of drives, and of thwarting of a drive.

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Temperature and Salinity Control of the Concentration of Skeletal Na, Mn, and Fe in *Dendraster excentricus*¹

ROBERT C. HARRISS² and ORRIN H. PILKEY³

SPECIMENS OF *Dendraster excentricus* (Escholtz), the common American Pacific coast sand dollar, were collected from 22 localities between mid Baja California and Vancouver Island (Fig. 1). Three tests from each of the 22 localities were analyzed for Na, Mn, and Fe, using an atomic absorption spectrophotometric technique. Fe was determined with an analytical precision of $\pm 3.0\%$ of the amount present. Mn was determined to $\pm 2.0\%$ and Na to $\pm 8.0\%$. Table 1 is a summary of the analytical results. (Chemical analyses were made in the Department of Geology, Rice University.)

The primary purpose of this investigation is to delineate the effects of the environmental parameters, temperature and salinity, on the skeletal concentration of Na, Mn, and Fe in *D. excentricus*. Such information can be of interest both from the standpoint of paleoecology and in the elucidation of calcification processes. Because a single monomineralic species was studied, mineralogical and physiological variables affecting test composition are relatively constant and environmental factors are emphasized. A second purpose is to contribute knowledge of the concentration of Na, Mn, and Fe in natural high-Mg calcites, about which little is known.

Previously Pilkey and Hower (1960) studied the Sr and Mg contents of tests of the same species of sand dollar. The Mg contents of *D. excentricus* tests appeared to be directly related to both temperature and salinity. The Sr con-

tent is inversely related to temperature and is unaffected by salinity.

Environmental data used in the present study are approximations based on extrapolation of data from points of known water conditions to specific collecting localities. Considerably more data on temperature than on salinity were available for this purpose. Unfortunately, it was possible to obtain low salinity specimens only at the end of the temperature range, which prevents observation of salinity effects over a wide temperature range.

The authors wish to express their thanks to Professor J. J. W. Rogers and C. W. Correns, who kindly read the manuscript, and to Mrs. Ilse Webb, who aided in statistical computations.

RESULTS

Figure 2 is a plot of the Na, Mn, and Fe content of *D. excentricus* tests vs. the mean summer temperature (mean temperature of the three warmest months at the various collecting localities). This measure of water temperature was chosen because in the previous study (Pilkey and Hower, 1960) the closest temperature-composition correlations were noted with reference to summer temperatures. Each point on Figure 2 represents an average concentration value based on analyses of three individual tests from each location. Because of the lack of precise salinity data, locations were classified simply as normal or low salinity. (For present purposes, low salinity is arbitrarily considered to be less than 32 ppt.) Normal and low salinity locations are designated by separate symbols in Figure 2. A third symbol is used for analyses of bay or quiet water forms which are recognized as a separate "ecological race" (Raup, 1958). All of the bay forms are also from low salinity locations. The trend lines in Figure 2 are least squares regression lines calculated using all of the data.

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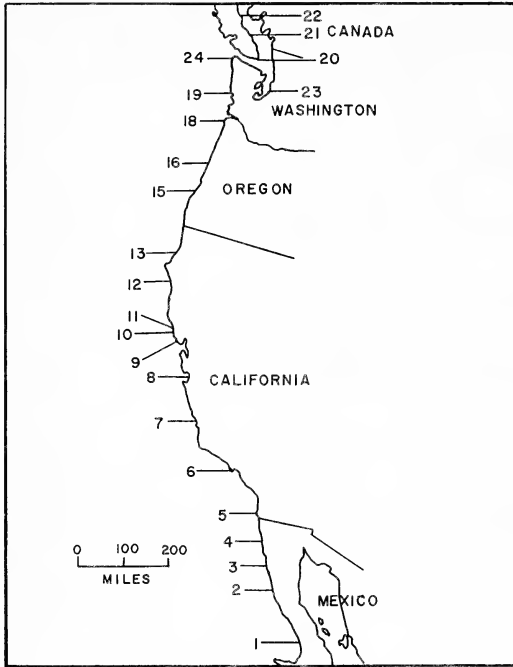


FIG. 1. Map showing approximate position of collecting localities.

Individual analyses of Na in *D. excentricus* tests ranged from 3,800 to 12,200 ppm, averaging 6,440. Mean values of three tests from each locality range from 4,100 to 10,600 ppm. Very few analyses of Na in the skeletons of other organisms are available for comparison with these data. The low-Mg calcite shells of the common oyster, *Crassostrea virginica*, generally contain between 2,000 and 3,000 ppm Na, which is somewhat lower than that observed in high-Mg calcite sand dollar tests. A direct relationship between the Na content and salinity was observed in oyster shells by Rucker and Valentine (1961), but this was not observed in sand dollars (Fig. 2); however, the oysters were collected over a much wider range of salinities.

The Mn content of *D. excentricus* tests range from 12 to 91 ppm and averages 35 ppm. The average concentration of the three tests from each locality ranges from 13 to 84 ppm. Figure 2 shows that the lowest values of Mn are found in tests from cold waters; the cold-water tests also exhibit the greatest variation in Mn

content. Salinity does not appear to affect the Mn content consistently. Judging from the few published figures on Mn in organic carbonate materials, the high-Mg calcite skeleton of *D. excentricus* contains Mn in intermediate amounts, i.e., lower than some figures reported for low-Mg calcite skeletons, higher than those reported for some aragonite skeletons (Rucker and Valentine, 1961; Pilkey and Goodell, 1963).

The Fe content of *D. excentricus* tests ranges from 140 to 620 ppm and averages 270 ppm. Location averages range from 187 to 573 ppm. Again, no strong temperature or salinity effect is apparent (Fig. 2). The concentration level of Fe in *D. excentricus* tests is similar to that noted in both low-Mg calcite and aragonitic skeletons of other organisms.

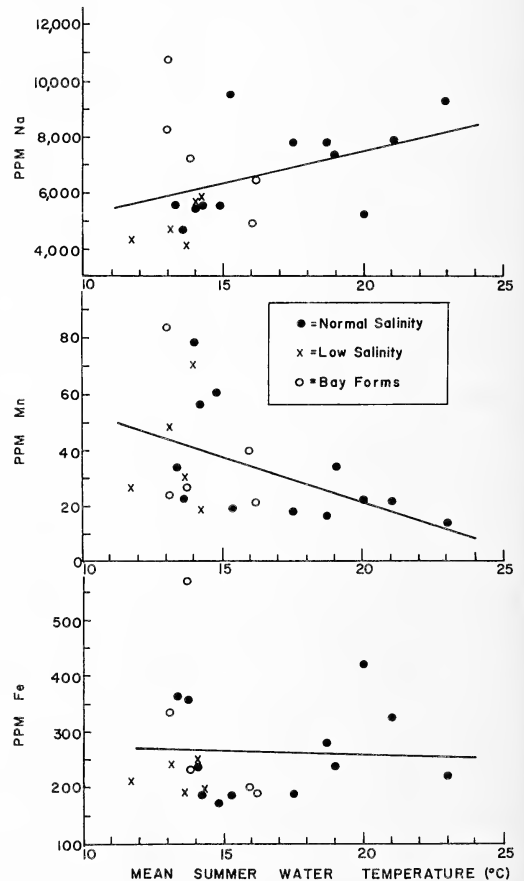


FIG. 2. The relationships between concentration of elements and mean summer water temperature.

TABLE 1
SUMMARY OF ANALYTICAL DATA

LOCATION				LOCATION			
NO.	Na	Mn	Fe	NO.	Na	Mn	Fe
1	8,200*	12	160	12	4,900	18	430
1	9,400	14	230	12	4,200	21	380
1	10,000	14	260	12	4,500	19	260
2	6,800	15	320	13	5,000	60	340
2	6,100	15	280	13	4,500	44	200
2	10,400	15	240	13	4,200	40	200
3	7,200	18	160	15	4,000	31	140
3	8,400	18	200	15	4,000	30	180
3	7,800	19	200	15	4,400	31	270
4	7,200	21	320	16	5,700	20	160
4	8,400	22	340	16	4,900	18	260
4	7,800	21	320	16	5,400	22	190
5	5,500	18	310	18	5,800	70	160
5	5,000	19	440	18	4,500	47	220
5	4,900	22	520	18	5,000	64	140
6	9,000	45	240	19	5,300	59	240
6	6,000	26	240	19	5,700	44	180
6	7,000	27	230	19	5,400	65	150
7	12,200	16	220	20	9,200	25	350
7	9,200	19	160	20	7,200	22	320
7	7,000	31	190	21	8,000	19	190
8	5,300	64	230	21	5,700	21	200
8	6,200	72	270	21	5,300	23	180
8	5,300	77	260	22	5,400	40	220
9	5,700	57	300	22	4,500	35	140
9	5,700	82	200	22	4,300	46	260
9	4,900	94	220	23	9,800	91	620
10	6,000	23	230	23	12,200	86	480
10	8,000	27	260	23	9,800	74	620
10	7,600	31	190	24	4,900	26	270
11	5,800	34	350	24	3,800	29	150
11	4,500	32	320	24	4,000	27	230
11	6,200	35	420				

* All quantities expressed as ppm.

DISCUSSION

Linear correlation coefficients were calculated for the relationships between composition and water temperatures. When using all the data, only the inverse Mn relationship is barely significant (95% confidence level). Removal of the bay forms from consideration results in a strong significant direct relationship between Na content and water temperature, but has little effect on the Mn curve. The Fe content exhibits no significant relationship with temperature. Distinct interpopulation differences in the concentration of these elements exist, but it is apparent that differences in temperature and

salinity are only partially responsible for these compositional differences. Other previously cited trace element studies of individual species, in which environmental effects were observed, also indicate that temperature and salinity differences are only partly responsible for compositional differences. Part of the problem in this and in the other studies has been the difficulty in estimating reliably the natural environmental conditions under which skeletal material was deposited. Furthermore, it may well be that presently unevaluated metabolic and crystal growth effects (which may or may not be related to external environmental condi-

tions) are important factors in the distribution of skeletal trace elements.

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Vertical Circulation Off the Ross Ice Shelf

C. W. THOMAS¹

ABSTRACT: The Ross Ice Shelf is a floating ice mass about 200 m thick over an average depth along the barrier of 567 m. In January the prevailing wind blows from the east, parallel to the coast. The wind current transports the low salinity layer (ca. 50 m) toward the ice shelf, where it must descend. Directly off the barrier we find low salinities to a depth of 150 m. The circulation here is quite similar to that defined by Sverdrup along the shelf ice of Queen Maud Land. Because of sinking of the low salinity layer near the barrier, diatoms live in abundance at subcompensation depths, *Trigonium arcticum* actually on the sea bed.

THE SOUTHERN BOUNDARY of the Ross Sea is fringed by floating ice of the Ross Ice Shelf except for the relatively small McMurdo Sound-Ross Island area. The clifflike barrier of the ice shelf is about 200 m thick (Sullivan, 1957). An average of 35 m rises from the surface of the water and about 165 m are submerged. The average depth along the barrier is 567 m. The width of the shelf in places exceeds 1300 km. Since water can circulate beneath this huge ice mass we can expect unique features of circulation.

The Ross barrier is washed by the Circumpolar Countercurrent which is produced partly by the distribution of density and partly by the prevailing wind. This current is usually weak along the barrier, but as it sweeps around Cape Adare it often attains a velocity of about 3 knots (author's observation). The data shown in Table 2 for station G-1 indicate that at this station a weak current is flowing toward the east. This supports the postulation of Kort (1962), who projected such a current through the vicinity of this station.

In all, three stations were taken off Kainan Bay (Ross Ice Shelf) along a north-south line at distances of 0, 40, and 156 km (Fig. 1). Two of these were taken in EDISTO and one in GLACIER. The work was carried out under the general supervision of Dr. Willis L. Tressler of the U. S. Navy Oceanographic Office. Several

vertical plankton tows were made with a 20-mesh closing net at stations Ed-1 and Ed-2. The water column was sampled at all three of these stations. The results of these casts are shown in Tables 1² and 2 respectively.

² Because of the wide variation in the size of biota the terms many, common, and few are used to denote relative quantitative abundance.

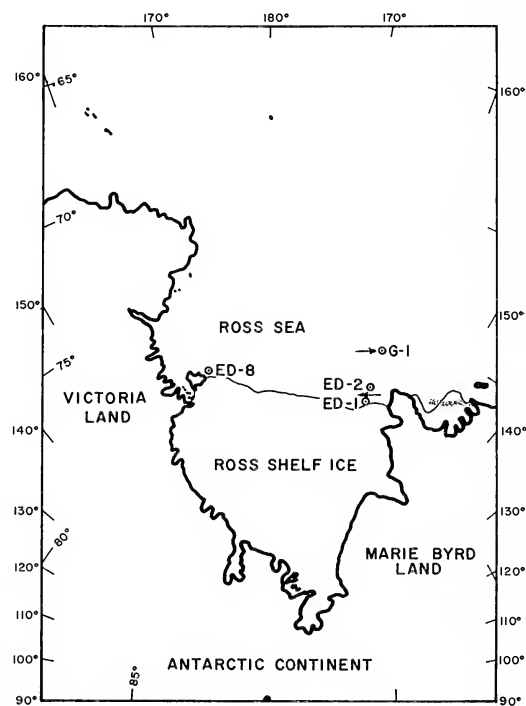


FIG. 1. Map showing locations of collecting stations.

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TABLE 1

INCIDENCE OF PLANKTON AS A FUNCTION OF DEPTH AT ROSS SEA STATIONS

ORGANISM	DEPTH AND INCIDENCE			
	0-100 m	100-200 m	200-300 m	300-400 m
Station Ed-1. Kainan Bay entrance. 78°10'S, 161°56'W. 0200 January 21, 1956. Depth, 732 m. Algae present throughout water column.				
<i>Coscinodiscus borealis</i>	few	none	few	none
<i>Coscinodiscus janishu</i>	few	none	none	none
<i>Coscinodiscus</i> sp. A	many	few	common	common
<i>Corethron criophilum</i>	many	many	common	common
<i>Streptotheca thamenis</i>	few	none	none	none
<i>Hemiaulus membranecus</i>	common	none	none	none
<i>Eucampia valasistum</i>	few	none	none	none
<i>Eucampia zoodiaius</i>	few	none	none	none
<i>Fragilariopsis antarctica</i>	common	common	none	none
<i>Thalassiosira</i> sp.	common	none	common	none
<i>Nitzschia seriata</i>	few	none	none	none
<i>Rhizosolenia alta</i>	common	none	none	none
<i>Rhizosolenia calcai avis</i>	common	none	few	none
<i>Peridinium depressum</i>	few	none	few	none
Copepods	none	common	many	few
Nauplii	none	common	many	few
Veligers	none	none	few	none

Station Ed-2. 40 km north of Kainan Bay. 77°44'N, 162°12'W. 1200 January 28, 1956. Depth, 700 m. Algae present in upper layers.

<i>Coscinodiscus borealis</i>	few	none	none	none
<i>Coscinodiscus janishu</i>	many	none	few	none
<i>Coscinodiscus</i> sp. A	common	none	few	none
<i>Corethron criophilum</i>	many	none	few	none
<i>Streptotheca thamenis</i>	few	none	none	none
<i>Hemiaulus membranecus</i>	common	none	none	none
<i>Eucampia zoodiaius</i>	few	none	none	none
<i>Fragilariopsis antarctica</i>	common	none	none	none
<i>Nitzschia seriata</i>	few	none	none	none
<i>Rhizosolenia calcai avis</i>	many	none	none	none
<i>Peridinium depressum</i>	few	none	none	none
Tintinnids	few	none	none	none
Copepods	none	none	many	none
Nauplii	none	none	many	none
Veligers	none	none	few	none

TABLE 1 (continued)

Station Ed-8. Off Cape Crozier. 77°29'S, 169°34'E. 0 600 February 28, 1956. Depth, 300 m. Algae present throughout water column.

<i>Coscinodiscus borealis</i>	few	none	none
<i>Coscinodiscus janishu</i>	few	few	few
<i>Coscinodiscus</i> sp. A	few	none	none
<i>Coscinodiscus</i> sp. B	common	few	few
<i>Corethron criophilum</i>	many	common	common
<i>Eucampia valasistum</i>	few	none	none
<i>Trigonium arcticum</i>	none	none	many
<i>Thalassiosira hyalina</i>	few	none	none
<i>Thalassiosira</i> sp.	few	none	none
<i>Fragilariopsis antarctica</i>	few	few	none
<i>Disephanus speculum</i>	common	few	few
<i>Peridinium depressum</i>	many	none	none
<i>Tomopteris</i> sp.	few	none	none
Copepods	common	few	many
Nauplii	many	many	many
Veligers	many	none	none

In addition to the three stations mentioned above one (Ed-8) was taken 1 km off Cape Crozier, Ross Island (Fig. 1). Opportunity did not permit taking additional stations offshore along the same meridian, normal to the current. The populations shown in Table 1 were living when taken and examined at stations Ed-1 and Ed-8. They were preserved for later examination at station Ed-2. The presence of diatoms at depths of 200-300 m and deeper engendered a desire to inquire into the reason for this apparent phenomenon.

The author is grateful to Dr. W. L. Tressler and to Mr. J. Q. Tierney, both of the U. S. Navy Oceanographic Office, for data and help in identifying biota.

DISCUSSION

According to Sverdrup (1953a) the threshold requirement in energy for *Coscinodiscus excentricus* is 0.002 lys. min⁻¹. Schreiber (1927) calculated 0.00172 lys. min⁻¹ for *Biddulphia mobiliensis*, the lowest energy requirement for a diatom of which there is a record. No micro-meteorological data were taken. However, List's tables (1951) show an albedo of 14% under average conditions similar to those which existed off the Ross Ice Shelf at the time of observation on January 21, with 0.383 lys. min⁻¹

refracted into the sea. Considerably less energy reached Cape Crozier on February 28—1 month later. To determine the compensation depth, the coefficient of absorption for visible radiation is calculated from the Poole-Atkins (1929) equation:

-k = 1.17.D⁻¹

where D = transparency by secchi disk (in meters).

-k = 4.2 × 10⁻³ cm with a transparency of 4.

The compensation depth is found from the equation:

z = (1/-k) ln (I_z/I_o)

where I_z = threshold requirement in energy (1.72 × 10⁻⁵ lys. min⁻¹), and I_o = energy refracted into the sea (3.83 × 10⁻¹ lys. min⁻¹).

Then: z = -12.65 m (compensation depth).

Because transparency in Antarctic waters is primarily a function of population densities, -k = 4.2 × 10⁻³ is valid only for the upper 4 m. However, considering the density of populations at lower depths, it is axiomatic that *Corethron criophilum*, for example, cannot be fixing carbon by photosynthesis at depths in excess of 300 m. Still, at station Ed-1 this diatom and *Coscinodiscus* sp. A occurred throughout all sampled layers of the water column. At sta-

TABLE 2
PHYSICAL ENVIRONMENT OF ANTARCTIC OCEAN PLANKTON STATIONS

DEPTH (meters)	TEMPERATURE (°C)	SALINITY (o/oo)	σ_t	$\Sigma\Delta D$	OXYGEN (ml/l)
Station Ed-1. Entrance of Kainan Bay. Color, 20. Transparency, 4.					
Surface	-0.50	33.93	2729	0000	10.94
50	-1.25	34.08	2744	0036	8.88
100	-1.66	34.15	2751	0066	8.22
150	-1.87	34.21	2756	0094	8.45
200	-1.91	34.22	2757	0120	8.48
300	-1.87	34.35	2767	0166	8.04
400	-1.83	34.39	2770	0205	7.85
500	-1.82	34.38	2770	0243	7.99
600	-1.83	34.47	2783	0277	7.90
Station Ed-2. 40 km north of Kainan Bay. Color, 20. Transparency, 4.					
Surface	0.47	34.21	2746	0000	10.59
50	-1.37	34.22	2755	0031	9.25
100	-1.78	34.27	2761	0056	8.23
150	-1.86	34.32	2765	0079	8.31
200	-1.88	34.39	2770	0100	8.04
Station G-1. 156 km north of Kainan Bay. Color, 14. Transparency, 9.					
Surface	-0.93	34.11	2745	0000	not
50	-0.60	34.15	2750	0030	observed
100	-1.72	34.23	2757	0057	
150	-1.75	34.29	2762	0082	
200	-1.79	34.32	2764	0104	
250	-1.85	34.31	2764	0127	
300	-1.89	34.31	2764	0149	
Station Ed-8. 1 km off Cape Crozier. Color, 20. Transparency, 3.					
Surface	-1.39	34.20	2754	0000	9.97
50	-1.39	34.27	2760	0026	9.88
100	-1.28	34.43	2772	0047	9.40
150	-1.16	34.31	2762	0068	9.60
200	-1.27	34.35	2766	0091	8.68
300	-1.86	34.54	2783	0119	8.61

tion Ed-8, off Cape Crozier, the diatom *Trigonium arcticum* was found only in the 200-300 m (bottom) cast. Moreover, it occurred in bottom surface samples together with fragments of decaying algae.

An investigation was then made of vertical circulation at station Ed-1, to determine if sink-

ing could account for these biota living beneath the compensation depth. According to Vowinkel (1957) the prevailing wind at Kainan Bay (Little America), Ross Ice Shelf, is easterly during the month of January. Considering the magnitude of the Coriolis force at this high latitude, it seems the light shallow layer would be trans-

ported toward the shelf ice under the influence of the wind stress. Continuity, then, requires a descending motion off the ice shelf. According to Sverdrup (1953*b*) this means that close to an ice shelf we can expect a thick layer of water of low salinity.

To determine the *rate* of sinking at station Ed-1, the procedure of Sverdrup (1953*b*) in his investigation of vertical transport of water in the vicinity of the ice shelf at Maudheim (Antarctica) was used:

$$T = \tau (s \, 2 \, \omega \sin \phi)^{-1} \dots\dots\dots (1)$$

where τ = stress of the wind, s = water density, ω = angular velocity of the earth, ϕ = latitude of the observer.

$$\tau = V^2 s^i K \dots\dots\dots (2)$$

where V = wind velocity, cm sec^{-1} , s^i = density of the air, K = factor of proportionality = 2.6×10^{-3} .

The equation becomes:

$$T = K s^i V^2 (s \, 2 \, \omega \sin \phi)^{-1} \dots\dots\dots (3)$$

According to Vowinckel (1957) the prevailing

wind at Kainan Bay (Little America) during the month of January is easterly. The average velocity is 10 knots or 510 cm sec^{-1} . Assuming this value for V and 78° for ϕ we obtain:

$$T = 7.0 \times 10^3 \text{ cm}^3 \text{ sec}^{-1} \dots\dots\dots (4)$$

where T = total volume of transport across a 1 cm-wide surface.

If sinking takes place uniformly from the barrier to an arbitrary distance of 10 km ($= 10^6 \text{ cm}$), the average downward velocity will be $7.0 \times 10^{-3} \text{ cm sec}^{-1}$. At this velocity water requires 14×10^6 seconds, or about 16 days, to sink 100 m. This is comparable with Sverdrup's calculation (1953*b*) of 20 days for 150 m at Maudheim. Probable circulation is shown in Figure 2.

Vertical circulation on the above scale can explain the presence of diatoms at subcompensation depths and elsewhere throughout the water column at Ed-1. While Cape Crozier is adjacent to the Ross Ice Shelf, a somewhat different pattern of circulation can be expected along a land

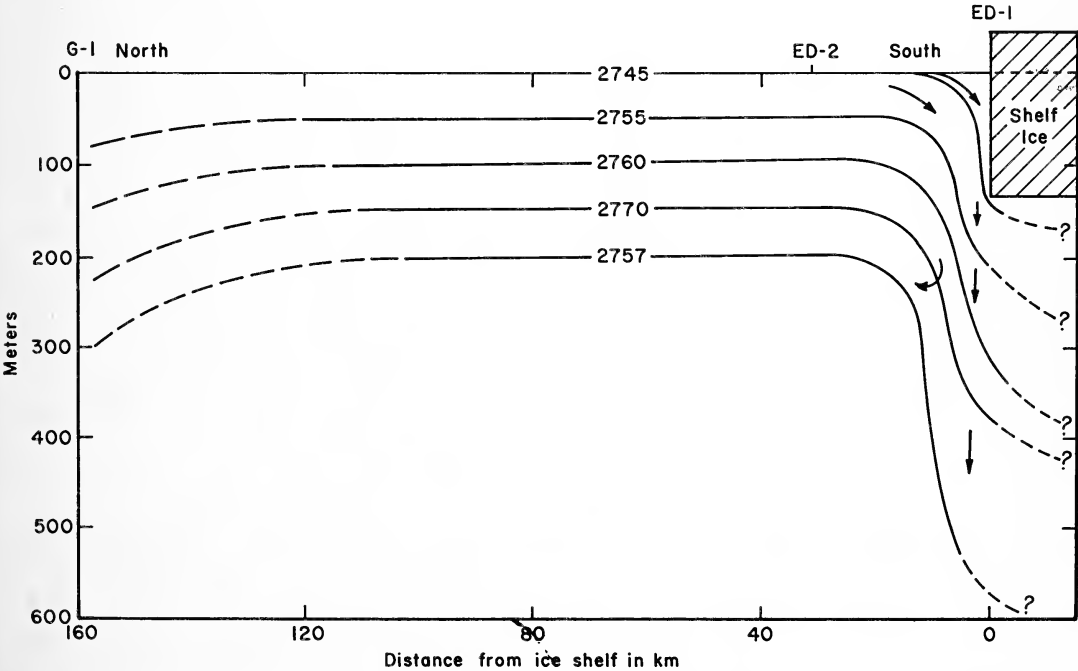


FIG. 2. Vertical section at right angles to the coast line in about 162°W , showing isopycnic lines. Probable vertical circulation is indicated.

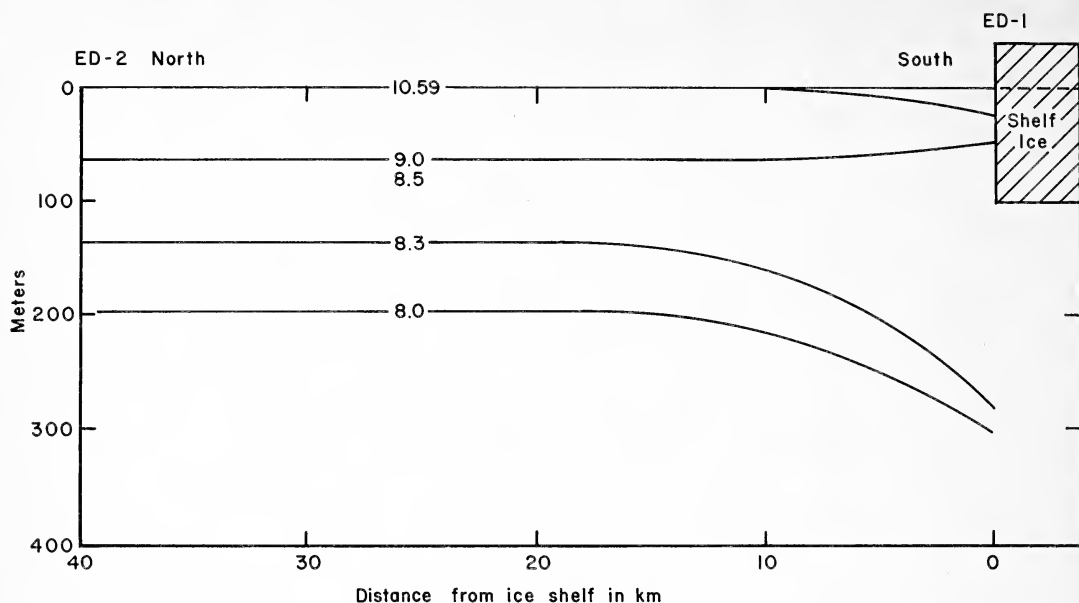


FIG. 3. Vertical section at right angles to the coast line in about 162°W , between stations Ed-1 and Ed-2 showing distribution of oxygen in ml/L.

mass. But plankton would, nonetheless, be swept past it in all layers. However, the diatom *T. arcticum* is found only on the bottom and nowhere else in the water column.

According to Hendy (1937) many specimens of *T. arcticum* spend most of the time as bottom forms and seldom get into the plankton. At several stations in Vincennes Bay the author found many on the bottom and none in the plankton. Hendy also mentions that many specimens are epiphytic on algae. How then can this plant fix carbon in the absence of radiant energy?

The fact that algae which appear to be decomposing are found in association with *T. arcticum* suggests the possibility of saprophytic nutrition. According to Kudo (1954) organisms (for example, *Euglena gracilis* and *Chilomonas paramecium*) receive saprophytic nutrition by diffusion through the body surface. This is accomplished without any organelles. There is only one known exception—marine dinoflagellates—in which saprophytic nutrition is accomplished through a special organelle. According to Dr. E. W. Putman³ (conversation),

T. arcticum may well be a saprophyte when not photosynthesizing.

An interesting by-product of this investigation is shown in Figure 3. The high content of oxygen in the surface layers is probably due to the abundant population of holophytic organisms.

CONCLUSIONS

The circulation pattern off the Ross Ice Shelf is nearly identical with that found by Sverdrup (1953b) to exist off the shelf ice of Queen Maud Land.

It is obvious to anyone interested in plankton ecology that organisms at subeuphotic depths cannot fix carbon and cannot be holophytic. Hence, *Trigonium arcticum*, under the conditions in which it was found, cannot fix carbon and be holophytic. This fact has been known at least since 1937 (Hendy). Still, no attempt has been made to explain how such plants do manage to live in virtual extinction of visible radiation. It is likely, then, that this diatom, and possibly others, may be capable of using chemical energy derived from decaying algae as a means of nutrition.

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A Comparative Study of *Craspedacusta sowerbyi* and *Calpasoma Dactyloptera* Life Cycles¹

DONALD C. MATTHEWS²

IN A PREVIOUS PUBLICATION (Matthews, 1963), immature medusae and mature hydranths of *Craspedacusta sowerbyi* were reported from aquaria of Mr. Mack Saki, a commercial guppy breeder of Honolulu. Whereas these medusae lived only three days, the hydranths persisted from October 1960 to November 1961 and, by hydranth and frustule budding, produced hundreds of hydranths, but no medusae.

Their reoccurrence on March 19, 1962 in aquaria of Mr. Saki (but not in mine) seemed again related to the water plant *Ceraptopterus thalictroides* (Matthews, 1963:20), but it harbored no hydranths. However, on internodes and leaf axils of *Elodea canadensis*, hydranths abounded. As before, immature medusae lived three days. The hydranths cultured in Petri dishes until December 1962 afforded material for continued study of factors reportedly responsible for medusa-bud formation.

Following Reisinger's (1934, 1957) methods, elevation of temperature from 20 C to 25–27 C failed to initiate medusa buds. Likewise, no maximal temperatures for hydranth, frustule, or medusa budding were found (McClary, 1959), nor were seemingly antagonistic budding stages altered either by feeding rates or temperature levels (Lytle, 1961). In short, cultures were cooled and warmed, starved and surfeited, isolated and crowded, coddled and coerced, without one medusa or tentacular hydranth resulting. As might be expected, no hydranths were living by December 30, 1962.³

Quite by chance, on 30 untreated "bunches"

of *E. canadensis* purchased March 3, 1963, atentacular and tentacular hydranths were observed. Although most atentacular hydranth stages of this study are from the Saki material, all tentacular hydranth stages are from this new source (March 3, 1963 to date).

For 18 months (March 1963 to August 1964) atentacular and tentacular hydranths have lived in my laboratory, either together in the same culture or isolated in separate cultures; and so striking is their resemblance that, although a tentacular hydranth stage of *C. sowerbyi* had not been mentioned previously (Browne, 1906; Crowell and Lytle, 1955; Dejar, 1934; Dunham, 1941; Fowler, 1890; Goette, 1909, 1920; Gaw and Kung, 1939; Hadzi, 1959; Kramp, 1950; Kuhl, 1947; Lytle, 1961; Matthews, 1963; McClary, 1959; Moser, 1930; Payne, 1924, 1926; Pennak, 1959; Potts, 1906; Reisinger, 1934; Romanes, 1881; Ryder, 1885; Uchida, 1955, 1963; and Woodhead, 1943), there seemed little doubt that this was but an aberrant form of a single, dimorphic species.

The purpose of this paper is threefold: (1) to verify Buchert's (1960) atentacular and tentacular stages, (2) to question, in light of my findings, the relationship he ascribes to certain of these stages, and (3) to report, for the first time in Hawaii, stages in the life cycle of *Calpasoma dactyloptera* (Fuhrmann, 1939).

IA. ATENTACULAR HYDRANTHS OF MIXED CULTURES

Small portions of *Elodea canadensis* with attached atentacular and tentacular hydranths were placed in Petri dishes containing 30 ml of aged tap water. Although some cultures were allowed to evaporate almost completely, most were maintained at the 30 ml level.

Temperatures varied from 20.5 C to 28.0 C, with the mean at 26.5 C. The pH ranged from

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³ While I was searching for new material, both atentacular and tentacular hydranths were undoubtedly present all the time in aquaria on my own lanai, where subsequently they were found!

6.5 for new cultures to 8.5 for old, well-established cultures, with the mean at 7.5.

The number of hydranths per culture was restricted by removal of frustules of 10 atentacular and 10 tentacular hydranths.

Cultures remained covered except when hydranths were observed or when an oligochaete (*Aeolosoma hemprichi*) and turbellarians (*Planaria* sp. and *Stenostomum tenuicaudatum*) were introduced (Nuttymcombe and Waters, 1938). These were directed by "minuten Nadeln" to make contact with a capitulum. Then, unlike small nematodes whose snake-like movements stopped as if the animal had been electrocuted (Matthews, 1963:20), *Planaria* continued to struggle even after its twisted, contorted body was completely ingested. Because a small worm usually filled a single hydranth's enteron, its constriction allowed the severed "posteriors" of large *Aeolosoma* and *Stenostomum* to gyrate blindly.

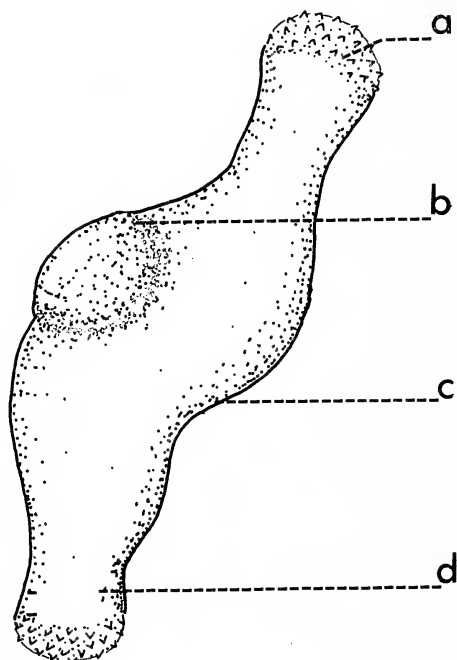
In colonies, unfed hydranths remained "hungry" even after ingested contents of fed hydranths cleared and presumably could have been freely shared. If clearing denoted digestion, it is interesting that it began just below the mouth and proceeded toward the attached basal portion. This was observed in a two-hydranth colony starved for three days and then fed *Planaria* whose pharyngeal region was gorged with carmen. Contact with one of the capitula was made at 7:50 AM. By 8:00 AM ingestion was complete and already the portion nearest the hydranth's mouth was beginning to clear. By 8:10 AM movement down the enteron had progressed halfway and, although the end nearest the hydranth's mouth was clear, the end farthest removed was only beginning to be so. By 8:30 AM the mass of carmen particles and the remains of the worm entered the base of the unfed hydranth, and by 10:00 AM had ascended one-third its column. The position of the mass as such did not further change. However, with digestion apparently completed, diffuse, minute red granules indicated that phagocytosis had also occurred.

This experiment was repeated the following day on the same colony. Once again ingestion required only 10 minutes and, as before, digestion seemed most pronounced in the region im-

mediately below the hydranth's mouth. Again, in $\frac{1}{2}$ hr the almost completely digested mass reached the base of the hydranth but, instead of entering the base of the other hydranth, it ascended the column just descended. And, although ascending the first half required almost 2 hr, ascending the last half, plus complete egestion, required only 10 minutes. As before, small red granules remained, indicating that some phagocytosis had taken place. Whether or not sharing occurred, the unfed hydranth instantly accepted a new worm whereas the fed hydranth repeatedly rejected it. This, however, may have been more the result of unspent nematocysts in the unfed hydranth and of spent nematocysts in the fed hydranth than the result of hunger per se.

Discussion pertaining to feeding tentacular hydranths is postponed until later.

Figures 1-4 are drawings of atentacular hydranths from which detritus and algae (*Tribo-*



0.3 mm

FIG. 1. *Craspedacusta sowerbyi*. a, d, Two atentacular hydranths; b, developing bud; and c, centrally located attachment point.

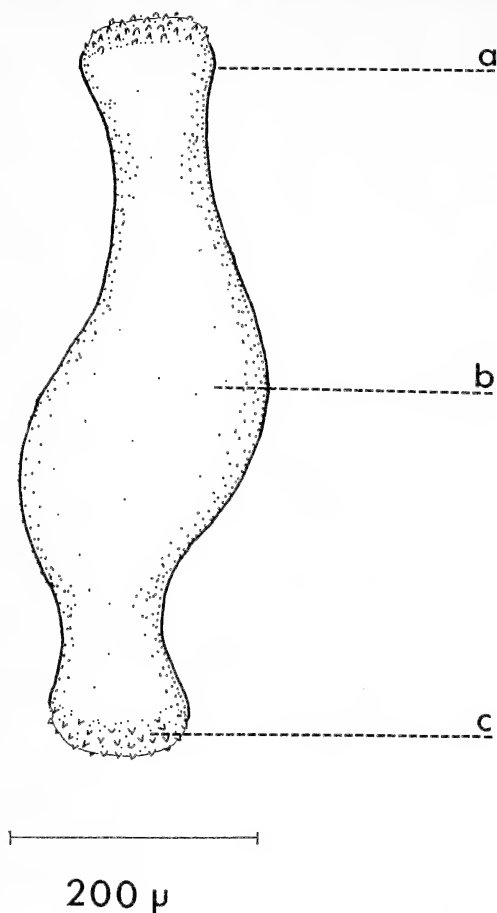


FIG. 2. *Craspedacusta sowerbyi*. *a*, *c*, Atentacular hydranths developing from both ends of the frustule; and *b*, attachment.

nema bombycina and *Fremyella diplosiphon*) have been removed. In Figure 1 the two atentacular hydranths (*a*, *d*) and the centrally located attachment point (*c*) correspond well with Buchert's stages (Fig. 13, row I), except that my developing bud (*b*) ultimately became a hydranth whereas his became a medusa (*a*). However, one need only refer to Payne (1924: 430, pl. 10) for confirmation of Buchert's row I stages.

Figure 2 with its two hydranths (*a*, *c*), its basal attachment region (*b*), and Figure 3 with its four hydranths (*a*, *b*, *c*, *e*) and its basal attachment region (*d*) correspond well with Buchert's stages (Fig. 13, row II). It should be pointed out, however, that my hydranths in

Figure 1 (*a*, *d*) and Figure 2 (*a*, *c*) are really not comparable with those of Figure 3 (*a*, *b*, *c*, *e*) or with those usually shown by other workers. As will be explained later, hydranth buds form as lateral outpocketings of existing hydranths, and thus size differences accompany age differences. Hydranths of Figure 1 (*a*, *d*) and Figure 2 (*a*, *c*) are of the same size and the same age. This will be explained subsequently under frustule development.

Figure 4 with its almost completely liberated frustule (*a*), its three hydranths (*b*, *c*, *e*), its attachment region (*d*), and Figure 5 with its two hydranths (*c*, *d*), its attachment region (*e*) on the node (*f*) of *E. canadensis* and its frustule (*b*) correspond well with those of Buchert's stages (Fig. 13, row III), although the actual site of frustule budding is different. Payne (1924: 430, pl. 10, fig. 64) also indicates that frustule budding occurs in the lower rather than in the upper one-third of the hydranth's column. Although the probable purpose of their figures was more to record frustulation than to depict its actual site, nevertheless, the hypostome region with its higher metabolic rate (Burnett, 1961: 427) is the one usually selected. Thus,

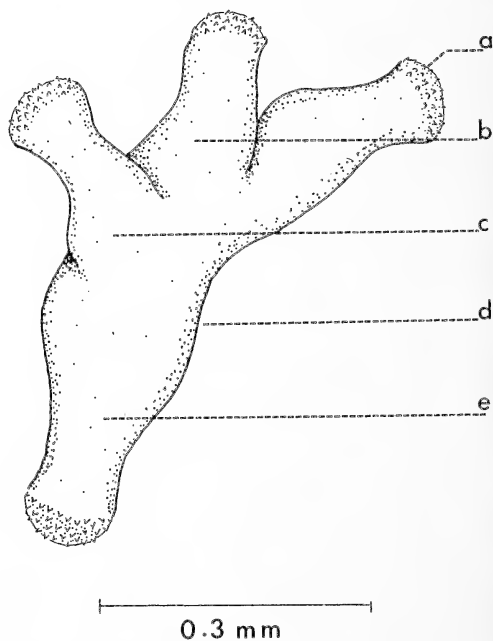


FIG. 3. *Craspedacusta sowerbyi*. *a*, *b*, *c*, *e*, Four atentacular hydranths; and *d*, attachment region.

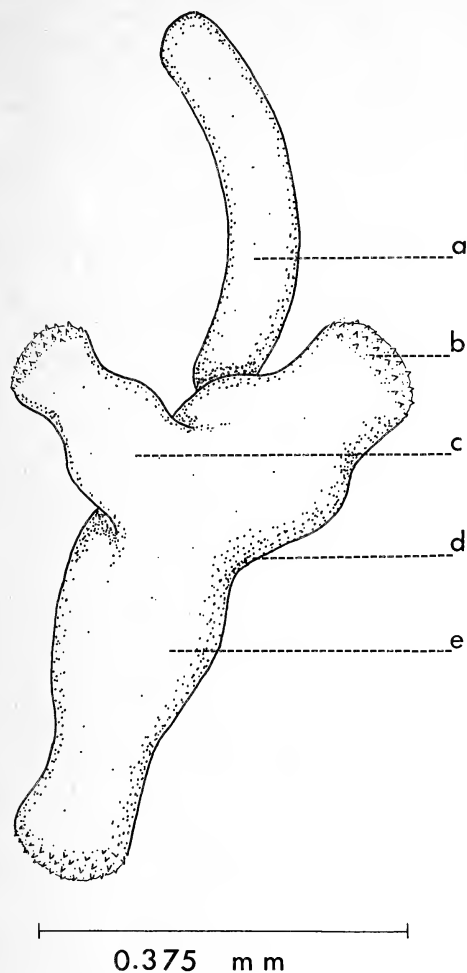


FIG. 4. *Craspedacusta sowerbyi*. *a*, Almost completely liberated frustule; *b*, *c*, *e*, three atentacular hydranths; and *d*, attachment region.

with the possible exception of frustule fragments and spherules, Buchert's stages (Fig. 13, rows I, II, III) add little that is new to our knowledge of *C. sowerbyi* atentacular hydranths.

IB. TENTACULAR HYDRANTHS OF MIXED CULTURES

As previously stated, small portions of *E. canadensis* placed in Petri dishes in 30 ml of aged tap water contained tentacular as well as atentacular hydranths. Thus, the conditions under which atentacular hydranths were observed apply equally to tentacular hydranths.

Figures 6, 7, and 8 show tentacular hydranths either as they occur naturally on stems and leaves of *E. canadensis* or as they appear on the bottom of Petri dishes with detritus and algae (*T. bombycina* and *F. diplosiphon*) removed. Thus, Figure 6*B*, *C*, and *D* represent tentacular stages which once occupied positions on a leaf of *E. canadensis* similar to those of tentacular stage *A*. However, in old, neglected cultures a thick algal mat may cover the bottom of the Petri dish and in, and frequently below, this mat tentacular hydranths are observed which are extremely hyaline. Near the bases of these old hydranths sometimes one, but frequently many, small spherules develop (Fig. 6*B*, *C*, *D*). From these metamorphose, after perhaps a month or more of delay, small tentacular hydranths. By this time the parent hydranth may be completely consumed. Thus, with the possible exception of body shape these stages (Fig. 6*A*, *B*, *C*, *D*) correspond well with those of Buchert's stages (Fig. 14, row IV).

Figure 7 represents frustule budding, a phenomenon frequently observed in young, vigor-

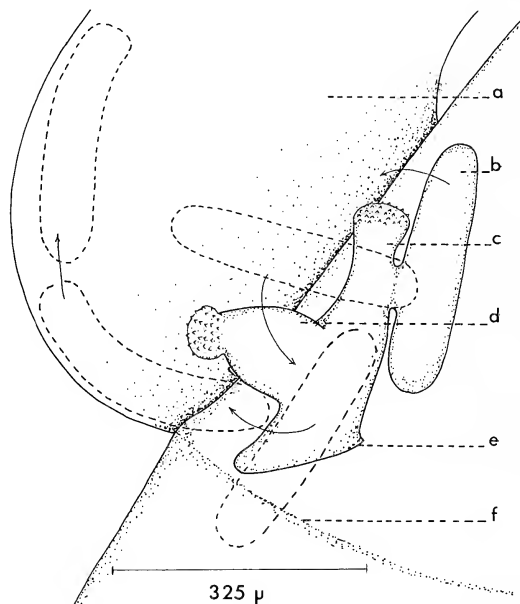


FIG. 5. *Craspedacusta sowerbyi*. *a*, A leaf portion of *Elodea canadensis*; *b*, budding frustule and its migration (arrows and dotted outline); *c*, *d*, two atentacular hydranths; *e*, attachment region; and *f*, nodal region of *E. canadensis* stem.

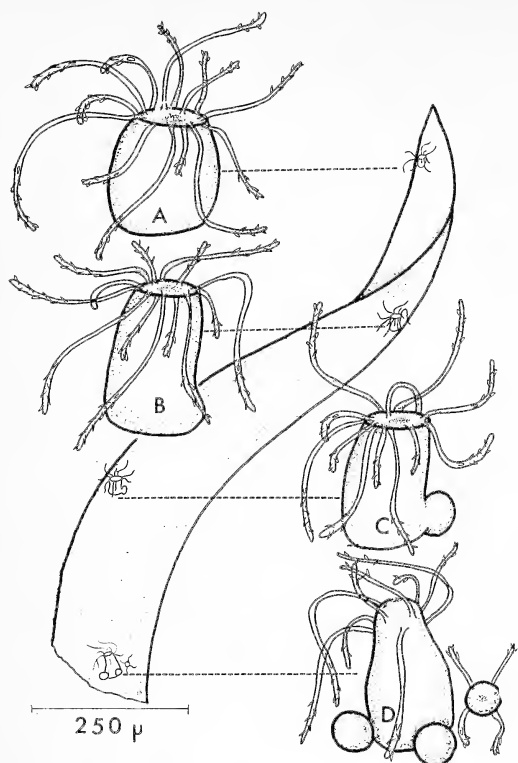


FIG. 6. Portion of *E. canadensis* leaf. A, Tentacular hydranth; B and C, tentacular hydranths forming spherules; and D, metamorphosis of a spherule into a small tentacular hydranth.

ous tentacular hydranths. This approximates frustule budding in atentacular hydranths, except that in tentacular hydranths the process may occur anywhere along the hydranth column, not necessarily near the hypostomal region. These small frustules may form spherules which develop tentacles (A); or may form tentacles directly at their thinner end (B); or may form tentacles simultaneously at both ends (C) even before the frustule attaches. Thus, from a frustule axle, tentacles may radiate like spokes from each end. Later, one end slowly rises from the bottom of the Petri dish and forms an asymmetrical V, i.e., one side is shorter than the other. Only when the complete metamorphosis from frustule to tentacular hydranth is observed can one say with certainty which is bud and which is parent. This, as previously stated, is quite different from true hydranth budding.

Again, except for slight differences in body

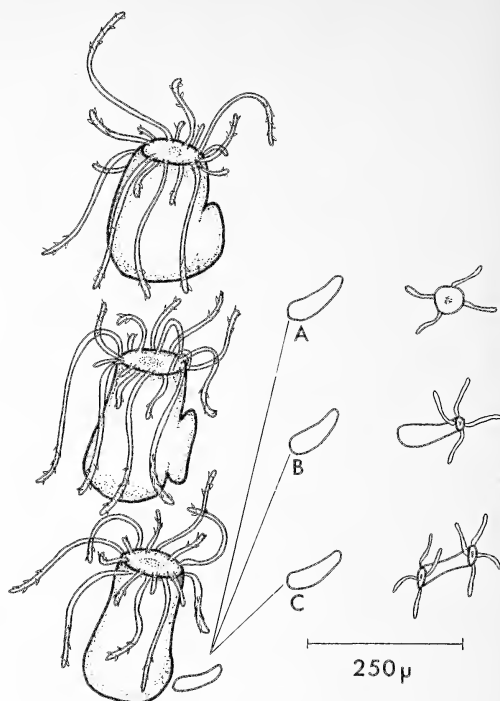


FIG. 7. Frustulation in a tentacular hydranth. A, Frustule forming a spherule with four tentacles; B, frustule forming a small tentacular hydranth; and C, frustule forming tentacles at both ends.

shape, these stages (Fig. 7A, B, C) correspond well with those of Buchert's stages (Fig. 14, row V).

Figure 8 represents a piece of *E. canadensis* on which hydranth-budding tentacular hydranths (A, B, C, D) and atentacular hydranths are located; the latter, for the sake of clarity, are omitted although in leaf axils of this very portion atentacular hydranths occurred. This point is stressed, for it is important that we realize that both tentacular and atentacular hydranths can occur simultaneously under the same environmental conditions.

Figure 8B is of particular interest because, since atentacular hydranths had apparently lost their ability to form medusa-buds, this function, I reasoned, had been taken over by small frustules (Fig. 8B, a). Food brought to tentacles elicited little or no response, but this was expected, since readiness to forage should have been preceded by movements of tentacles and velum. I waited. Days passed. Impatient at the

rate of metamorphosis, I freed with dissecting needles a "medusa" like that indicated by *A* and brought it to the surface. It sank slowly without so much as a single twitch. Rather than medusae metamorphosing from small frustules (*B, a*) these were, in reality, tentacular hydranths whose buds (*B, a*) developed tentacles and remained attached (*C, b* and *D, c*).

Thus, stages in tentacular hydranth budding (Fig. 8*A, B, C, D*) are comparable to those figured by Buchert (Fig. 14, row VI). It is some consolation now to learn that Buchert, too, first thought these "were larval forms out of which the medusa develop" (Buchert, 1960: 34).

Thus, all of Buchert's atentacular (type A)

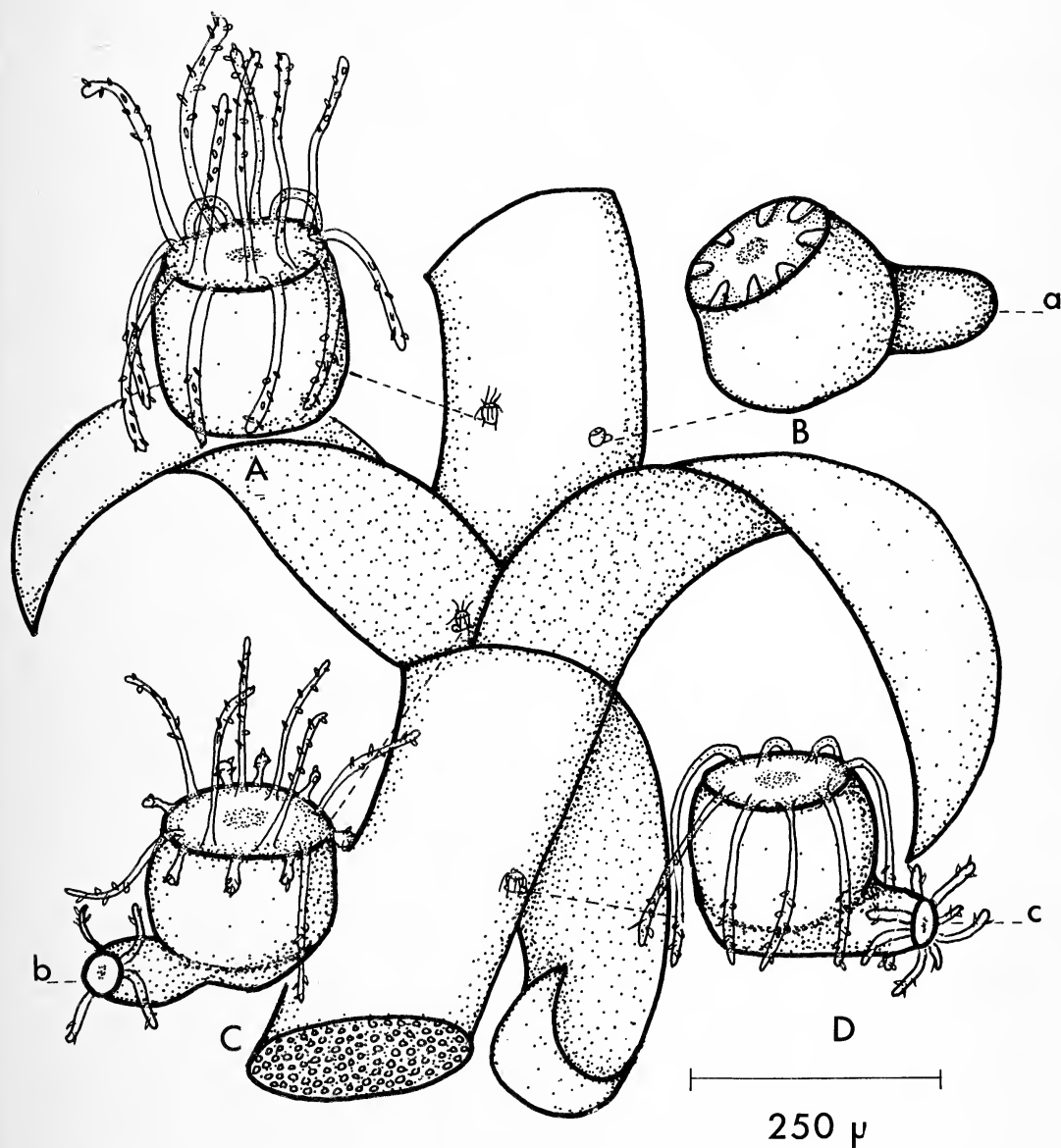


FIG. 8. Portion of *E. canadensis*. *A*, Medusa-like, tentacular hydranth; *B*, small, medusa-like hydranth with contracted tentacles and young bud (*a*); *C*, tentacular hydranth and bud (*b*) with four tentacles; and *D*, tentacular hydranth and bud (*c*) with eight tentacles.

and tentacular (type B) stages are accounted for. Although this strengthens his one species concept, its proof rests in: (1) the ability to demonstrate conclusively that frustules (Fig. 13 *A-B*) or frustule fragments (*C*) of atentacular hydranths can metamorphose into tentacular hydranths (Fig. 14*A*), and (2) that tentacular hydranths (Fig. 14*B*) can metamorphose into atentacular hydranths (Fig. 13*D*). If this cannot be demonstrated, then two similar but different species must exist.

To prove or disprove this, a more detailed and accurate study of frustules was needed. Previously, these had been collected from mixed cultures; now they must be obtained from cultures rigorously isolated. Therefore, careful precautions were taken against contamination.

II. THE RELATIONSHIP BETWEEN CERTAIN ATENTACULAR AND TENTACULAR STAGES

A complete set of equipment was placed in each of separate but adjoining rooms in the laboratory. This consisted of Petri dishes, pipettes, dissecting needles, thermometers, etc. Each set remained in its respective room and was checked before each day's work. Each room had its own *Aeolosoma hemprichi* cultured on rice-agar plates following the method of Brandwein (1937), and its own supply of aged tap water and pond water filtered through millipore filters of 0.45 μ pore size.

Although they were not absolute safeguards against contamination of one culture with another, results proved these precautions adequate.

Frustules were collected and cultured from previously isolated cultures. The number of atentacular and tentacular cultures was restricted to 20 each, from which the following information was obtained: (1) type of culture; (2) length, width at thicker end, width at thinner end; (3) change in shape; (4) size of frustule divisions; (5) change in position (i.e., horizontal to vertical); (6) change in location (i.e., locomotion; and (7) date of capitulum or tentacle formation.

Previously, measurements in microns of the first frustule observed in each of 20 mixed cultures showed these variations: lengths 575–75, mean 375; widths, thicker end 125–37, mean

87; widths, thinner end 75–37, mean 54.

Figure 9*A* shows this frustule drawn to the same scale as other frustules. Measurements in microns of frustules from isolated atentacular hydranths (before any division of these frustules occurred) showed these variations: lengths 575–375, mean 465; widths, thicker end 125–100, mean 106; widths, thinner end 100–75, mean 83. Figure 9*B* shows the size of this frustule drawn to the same scale.

Although division was observed in frustules measuring 575–425 μ , no division was observed in frustules measuring 375 μ . The following five examples are typical of frustule lengths and the lengths of pieces into which they divided:

LENGTH OF FRUSTULE (μ)	LENGTH OF PIECES (μ)	
	Short	Long
575	150	425
500	175	325
425	175	250
400	150	250
400	150	250

The short pieces showed these variations (measurements in microns): lengths 175–150, mean 160; widths, thicker end 75–55, mean 65; widths, thinner end 50–37, mean 42. Figure 9*C* shows the size of the small frustule fragment drawn to the same scale.

The large pieces showed these variations (measurements in microns): lengths 425–250, mean 300; widths, thicker end 100–75, mean 82; widths, thinner end 75–37, mean 54. Figure 9*D* shows the size of the large frustule fragment compared to sizes of other frustules.

Buchert (1960:47) lists the following variations for his Type A (atentacular) frustules (measurements in microns): lengths 635–441, mean 475; widths, thicker end 134–96, mean 118; widths, thinner end 96–76, mean 88. Figure 9*E* shows the size of this frustule compared with sizes of other frustules. Although these data do not lend themselves to statistical analyses, they do suggest some interesting possibilities.

Frustule *A* is smaller than frustule *B* because

mixed cultures would contain fragments of atentacular frustules and (as will be shown directly) small frustules of tentacular hydranths. In isolated cultures of atentacular hydranths, where frustules are allowed to divide before samples are taken, Figure 9B would approximate A. Since my selected B frustule so nearly approximates Buchert's E, one might assume that Figure 9E frustules were also selected before any of them divided (Fig. 13A-C).

Measurements in microns of the first frustules observed in each of 20 isolated, tentacular cultures showed these variations: lengths 225-75, mean 150; widths, thicker end 75-50, mean 55; widths, thinner end 50-37, mean 45. Figure 9F shows the size of this frustule compared with

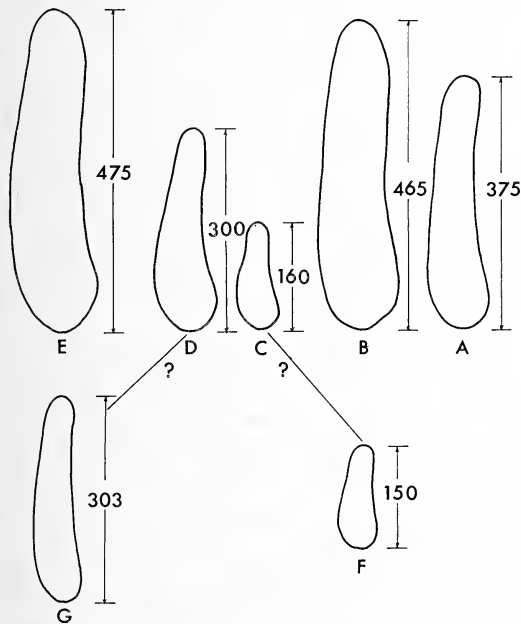


FIG. 9. Schematized frustules drawn to the same scale. A, Mean length and widths (thicker end, thinner end) of the first frustule observed in each of 20 mixed cultures; B, mean length and widths of first frustules observed from isolated atentacular hydranths before any division of frustules occurred; C, small fragment of a frustule; D, large fragment of a frustule; E, Buchert's atentacular frustule; F, tentacular frustule; and G, Buchert's tentacular frustule. (Question marks suggest possible relationships between C-F and D-G.) All measurements are in microns.

sizes of other frustules. Buchert (1960:47) lists the following variations for his Type B (tentacular) frustules (measurements in microns):

lengths 442-172, mean 303; widths, thicker end 78-48, mean 62; widths, thinner end 58-38, mean 48. Figure 9G shows the size of this frustule compared with sizes of other frustules.

Even without the application of statistical analyses the similarity of small fragment Figure 9C with frustule Figure 9F is striking, and suggests quite convincingly how one might be mistaken for the other. This is undoubtedly what I had done. I have no explanation why Figure 9G (Buchert's tentacular frustule) more nearly approximates Figure 9D (except for thicker width of D) than it does Figure 9F.

This much is now known: In isolated atentacular cultures, not only do large frustules (Fig. 9B) metamorphose directly into atentacular hydranths, but, more important, so do their fragments (Fig. 9D, C). Furthermore, in isolated tentacular cultures frustules metamorphose only into tentacular hydranths.

Change in frustule shape is considered here for two reasons: (1) its relation, if any, to frustule fragmentation, and (2) its relation to locomotion. Frustules of both atentacular and tentacular hydranths exhibit peculiar waves of contractility which slowly pass from one end of the frustule to the other. Figure 10 is a diagrammatic representation of these waves as observed in a 525- μ frustule of an atentacular hydranth. (In the figure, numbers correspond to ocular micrometer spaces of 25.) When first observed (Fig. 10A), this frustule appeared as if about to divide into a fragment 150 μ long, and a fragment 375 μ long; however, 15 minutes later the region of contractility had moved 100 μ (Fig. 10B). In another 5 minutes the region of contractility had moved an additional 75 μ (C); 5 minutes later another 75 μ brought the area of contractility to within 125 μ of the wider end (D). Then, 9 minutes later, the wave of contractility had completely traversed the frustule (E)—in the observed elapsed time of 34 minutes. If one adds another 10 minutes for the wave to reach the point where first observed (A), 45 minutes would be a conservative estimate of the time required for a wave to traverse the entire length of the frustule. Rarely, however, is frustule change of shape so simple. Figure 10F, G, and H clearly show that more than one wave may be operative and, although

these were not accurately timed, their rates appeared to be synchronized. This is much slower than the rate of contractility recorded for *C. sowerbyi* frustules by other workers (Crowell and Lytle, 1955:255). Furthermore, although this process may have something to do with locomotion, the contractile waves associated with Figure 10D, E, F, G and H are those of a frustule already attached. While certain of these contractile waves (Fig. 10E, F, G, H) might serve to carry developing nematocysts into the forming capitulum, other waves seem to carry materials in the opposite direction; thus their function remains obscure. Fifteen hours later the once horizontal frustule had assumed a vertical position and already a capitulum was formed. No divisions occurred.

On October 23, 1963, five atentacular colonies were placed in approximately 20 m/c of Zn^{65} diluted with 30 ml of filtered culture water. The purpose of this experiment was to follow "hot" frustules through several generations in an attempt to prove that, in mixed cultures, only atentacular hydranths would be radioactive. A reciprocal experiment was planned for the frustules of tentacular hydranths. These experiments

are being repeated, using a Packard Tri-carb liquid scintillation counter and weak (low energy) Betas in the hope that the possibility of knocking out tentacle-forming mechanisms might be lessened.

Figure 11 shows frustule budding and locomotion which occurred on October 30, 1963 in three of five radioactive, atentacular hydranths. This is included not because it is normal but, since the process is exaggerated, because a possible method of locomotion is suggested which normally cannot be seen. Culture 5 contained a large frustule 575 μ long, 100 μ wide at its thicker end, and 75 μ wide at its thinner end. As illustrated, this frustule (B) when observed at 10:20 AM lay some 2 mm removed from the hydranth (A) from which it budded, yet it was still connected by an extremely delicate, but nevertheless distinct, "mucus" tube whose diameter was approximately 50 μ . By 11:00 AM this frustule slowly changed from a horizontal to a vertical position, only to assume again a horizontal position with its smaller end pointing away from B. By 4:00 PM it had moved to point C some 825 μ from B. Here, as at B, it slowly righted itself, only to assume again a horizontal

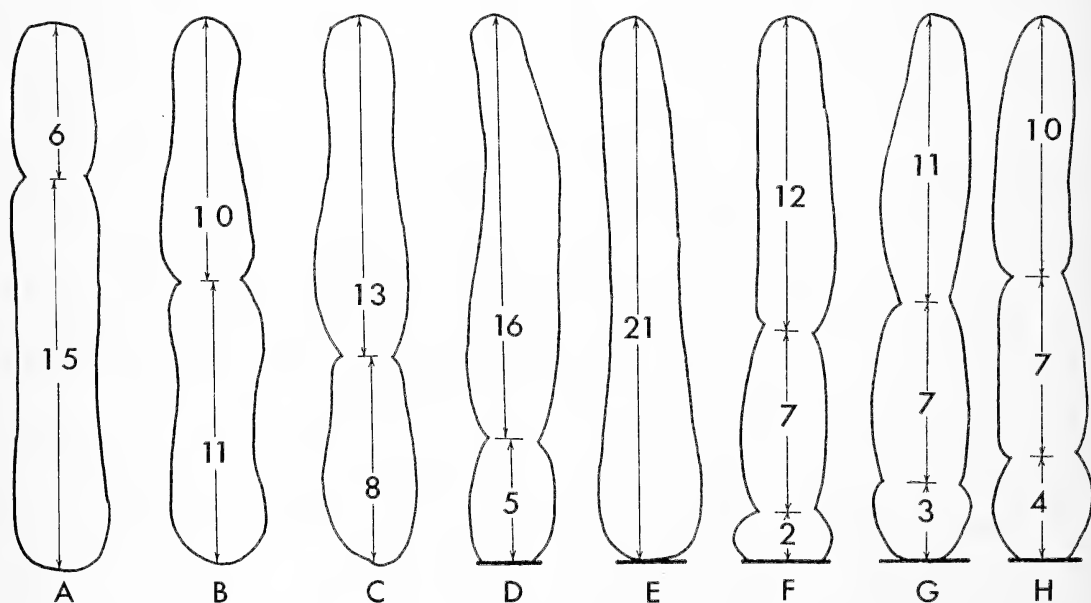


FIG. 10. Schematized drawing of frustules. A, B, C, and D, Changes in shape due to wave of contractility; E, failure of frustule to fragment; and F, G, and H, more than one wave operative. (Numbers correspond to ocular micrometer spaces of 25 μ and base line under D, E, F, G, and H signify attachment.)

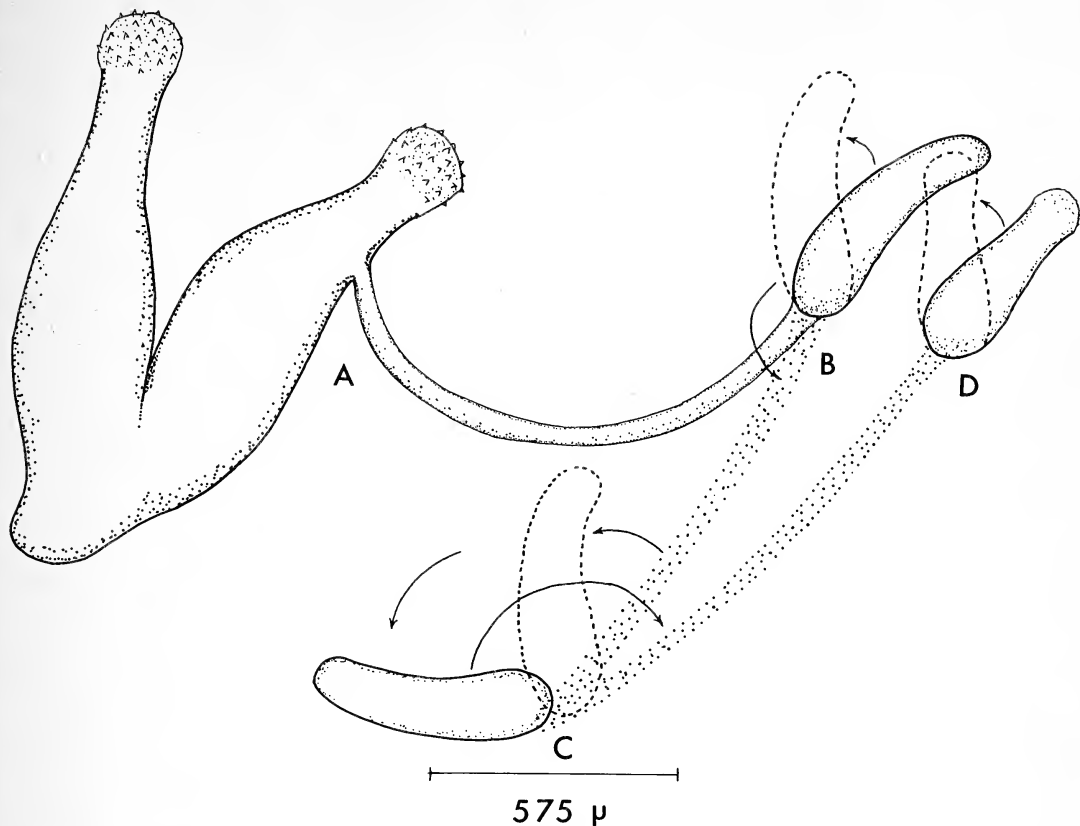


FIG. 11. Atentacular hydranth budding and frustule locomotion. *A*, Atentacular hydranth; *B*, frustule, horizontal (and dotted, vertical) at end of mucus tube; *C*, position of frustule at end of mucus carpet (*B*–*C*); and *D*, frustule attachment point at end of mucus carpet (*C*–*D*).

position with its smaller end pointing away from *C*. Next morning at 8:10 AM it had arrived at point *D*, about 850 μ from *C* and only about 175 μ from *B*. The thicker end was already attached, but the thinner end was elevated from the bottom of the Petri dish at about a 45° angle. It was no longer bean-shaped and was slowly metamorphosing into a young atentacular hydranth. It was now only 375 μ long and 125 μ wide at the thicker end; the thinner end still measured 75 μ wide. Next day, with the righting process completed, a capitulum developed. Exceedingly small, unidentified protozoa could be seen in the disintegrating tube between *A* and *B*. Regions between *B*–*C* and *C*–*D* lacked a lumen and thus were carpet-like. Toluidin blue (1:10,000) stained both tube and carpet very lightly, but in two days neither

was visible. Although this copious secretion was probably the result of Zn⁶⁵ irritation, it is interesting that the frustule seemed to be more affected than the hydranth. The frustule's decrease in size and its abrupt, almost opposite change in direction support this view. Also, its change of position from horizontal to vertical and vice versa seems more related to mucus changes than to changes of buoyancy.

Frustules of untreated hydranths also remain attached for some time, but in no instance is their attachment so pronounced. In most instances, although the remaining connection could not be seen, its presence could be demonstrated by passing a small dissecting needle between hydranth and frustule.

During Part II of this study many stages were observed which at first sight strengthened the

contention that tentacular hydranths (Buchert's line V) metamorphosed into atentacular hydranths (Buchert's line II). Figure 12 is a diagram of a large tentacular hydranth which already has "absorbed" one row of its tentacles (which row would be pure speculation). Each tentacle is roughly $75\ \mu$ long and is further characterized by its swollen, almost spherical distal end. Because of the migration of nematocysts, these tentacles are extremely hyaline except distally, where three or four nematocysts often re-

main. Figure 12B is a diagram of the tentacular portion of another hydranth in which only 2 tentacles in the bottom row and 6 tentacles in the top row remain. Figure 12C is a diagram of a hydranth in which 10 stublike tentacles remain, but it is difficult to determine which stub belongs to which row. All are completely devoid of nematocysts. In Figure 12D only 5 stubby tentacles remain and, again, all are perfectly clear.

In these and other examples hydranths, teeming with bacteria and protozoa, became milk-colored and in a few days disintegrated. Not once did loss of tentacles result in development of atentacular hydranths.

Since neither (1) the ability of frustules or of frustule fragments of atentacular hydranths to produce tentacular hydranths nor (2) the ability of tentacular hydranths to metamorphose into atentacular hydranths can be demonstrated, the one-species concept lacks cogency.

III. *Calpasoma Dactyloptera* IN HAWAII

To my knowledge, this species has been reported only by Fuhrmann (1939, Switzerland), Buchert (1960, Hungary), Lytle (1960, Indiana, USA), and Rohat (1961, Israel), but because it is associated with *C. sowerbyi* it probably will be found to be quite common.

For the most part, Fuhrmann's original description (1939:365) fits well the Hawaiian representatives of this species. The general body size and shape, and the arrangement of the two rows of tentacles follow Fuhrmann's description as do the number, size ($8-9\ \mu$), and arrangement of nematocysts.

In all likelihood Fuhrmann had not made a study of the life cycle, which probably accounts for his statement, "We have seen only isolated individuals. The polyp does not appear to reproduce by budding, but mainly by transverse division. In fact, we have seen several polyps which show a constriction in the middle of the body which appears to be the start of this phenomenon" [author's translation]. It is also unfortunate that Buchert, who studied the life cycle and observed the budding of spherules, frustules, and hydranths, failed to place these in the correct species, because of lack of isolation of cultures.

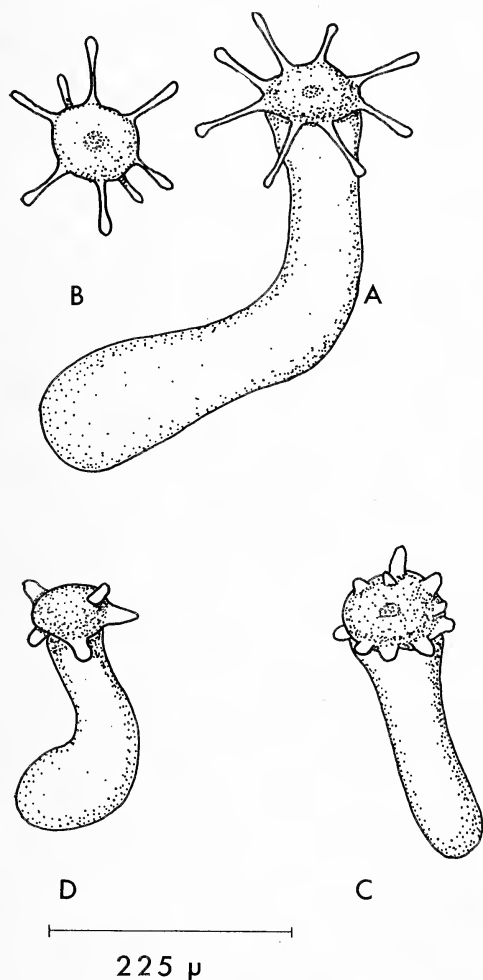


FIG. 12. Degeneration of tentacular hydranths. A, A large hydranth with but one row of tentacles; B, diagram of tentacular portion of hydranth with only two tentacles remaining in bottom row and six in top row; C, tentacular hydranth with only stublike tentacles remaining; and D, tentacular hydranth with only five, empty tentacle stubs remaining.

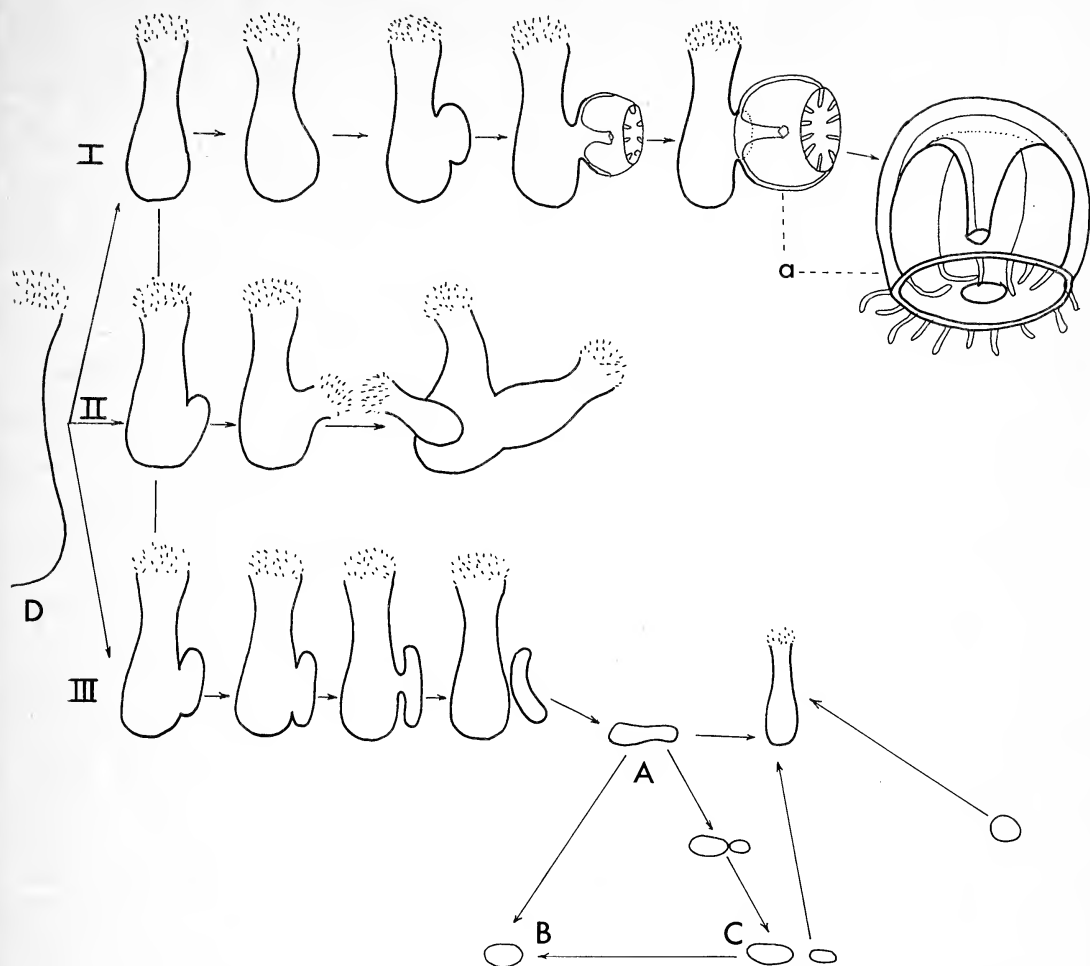


FIG. 13. Reproduction of Buchert's figures. Row I, medusa bud (*a*) formation; Row II, atentacular hydranth budding; and Row III, frustule budding. A-B and C-B indicate pathways by which tentacular hydranths are formed.

The study is by no means completed. As early as 1939, Fuhrmann (1939:368) said, "It is very probable that, under favorable conditions, the polyp forms a medusa like *Craspedacusta*." In light of the variability of published photographs and drawings of *Craspedacusta* medusae, this suggestion has real merit.

Likewise, there is need for up-to-date, electron microscope studies of chromosome numbers in frustules. Although White (1930:230) states: "There seem to be twelve chromosomes at each pole of late anaphase of the primary spermatocyte," this number could not be verified in frustules since aceto orcein- and Feulgen-stained squashes (the latter, colchicine-

pretreated) failed to reveal mitotic figures. The removal of cytoplasmic RNA by ribonuclease is now being attempted, in the hope that only the DNA of the nucleus will take up the stain.

ACKNOWLEDGMENTS

I wish to express indebtedness to our staff artist Mr. Robert A. Kinzie who prepared the figures for publication. I wish also to acknowledge with thanks the identification of algae by Dr. M. S. Doty. Likewise to Dr. Voss, for information pertaining to the rather obscure Buchert paper, I am deeply grateful. I wish also to express my appreciation to Dr. Donald Cutress,

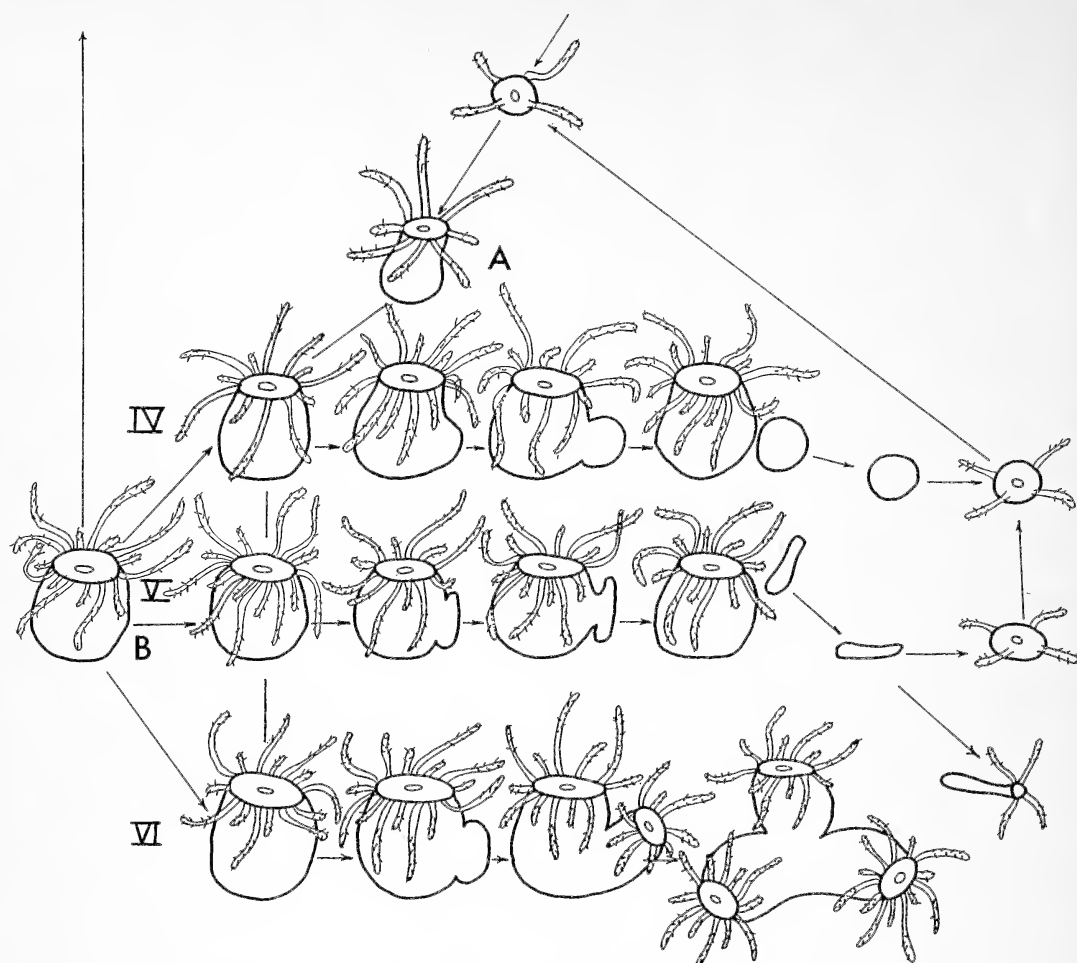


FIG. 14. Reproduction of Buchert's figures. Row IV, production of tentacular hydranths from spherules; Row V, frustule budding and formation of tentacular hydranths; and Row VI, tentacular hydranth budding. A indicates tentacular hydranth connecting atentacular and tentacular stages, and B indicates tentacular hydranth connecting atentacular stages (Fig. 13D).

whose generous hospitality enabled certain of us attending the XVI International Congress of Zoology to meet and to discuss *Craspedacusta*. I wish to credit Dr. Yanagita for improving the reliability of my nematocyst measurements. Above all others, I wish to thank Dr. C. F. Lytle who, although about to publish an account of tentacular hydranths which appeared in his culture of *C. sowerbyi* while he was at Indiana University, graciously forwarded copies of the papers by Buchert (1960), Fuhrmann (1939), and Rohat (1961).

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NOTE

Bleekeria compta: A New Binomial for a Hawaiian Apocynaceous Tree

ROBERT L. WILBUR¹

THE SMALL VARIABLE TREE called the *holei* by the Polynesian natives occurs in the drier portions of the Hawaiian Islands. In the scientific literature it has been referred to most frequently as *Ochrosia sandwicensis*, but unfortunately this long-used binomial cannot be maintained. Alphonse DeCandolle (Prodr. 8:357, 1844) proposed the name, but his original description ("foliis obtusiusculis, bracteis basi denticulatis") and the cited synonymy (*Cerbera parviflora* sensu Hook. and Arn.) indicate that he was again describing *Rauvolfia sandwicensis*, which he had first published earlier in the same work (Prodr. 8:339, 1844). Hillebrand (Fl. Haw. Is.: 295, 1888), Schumann (Pflanzenfam. IV, 2:153, 156, 1895), Rock (Indigenous Trees Haw. Is.: 409, 413, 1913), however, all recognized the actual identity of DeCandolle's species and therefore attributed the name *O. sandwicensis* to Asa Gray. Gray (Proc. Am. Acad. 5:333, 1861) misunderstood DeCandolle's concept of the species, and applied the name to the *holei* and not to the *hao* (*Rauvolfia sandwicensis*), as did DeCandolle. Gray's usage, of course, has no nomenclatural validity. Hillebrand (Fl. Haw. Is.: 297, 1888) described a little-known variant from the Nuuanu Valley of Oahu as the β variety of *Ochrosia sandwicensis* A. Gray, while Schumann (Pflanzenfam. IV, 2:153, 156, 1913), after examining Hillebrand's specimen at Berlin, considered it a distinct species and provided the binomial *O. compta*. For those who, like Fosberg (in Zimmerman's Insects of Hawaii 1:114, 1948), recognize only one species within the variable Hawaiian populations and whose concept of *Ochrosia* includes those species with

a nonfibrous mesocarp, the proper binomial is *Ochrosia compta* K. Sch.

Recent students of the Pacific flora, such as Koidzumi (Bot. Mag. Tokyo 37:52, 1923), Markgraf (Engler's Bot. Jahrb. 61:168, 1928), Merrill and Perry (J. Arn. Arb. 24:213, 1943), and Smith (Bull. Torrey Club 70:549, 1943), have accepted as genera the two groups recognized by earlier workers as sections or subgenera of *Ochrosia*. The entire group sorely needs monographic attention, but until this needed task is accomplished it would seem best to follow those students whose more detailed studies have convinced them of the generic distinctness of the two groups of species.

The Hawaiian species belongs to the group with nonfibrous mesocarps and with a conspicuous longitudinal cavity in the remnant of the partition of the fruit. It is therefore a *Bleekeria*. Koidzumi (Bot. Mag. Tokyo 37:52, 1923) first recognized this and provided the new combination *Bleekeria sandwicensis*. Koidzumi's binomial cannot be salvaged, under the provisions of Article 72 of the International Code (Reg. Veget. 23:52, 1961), since there is an available legitimate specific epithet: *Ochrosia compta* K. Sch. Therefore a new combination under *Bleekeria* is necessary.

Bleekeria compta (K. Sch.) comb. nov.

Ochrosia sandwicensis β var. Hbd., Fl. Haw. Is.:297, 1888.

Ochrosia compta K. Sch., Nat. Pflanzenf. IV, 2:156, 1895.

Bleekeria sandwicensis (sensu A. Gray [non A.DC]) Koidz., Bot. Mag. Tokyo 37:52, 1923.

The type of this species was undoubtedly lost in the bombing of Berlin in 1943. Schumann based the species upon Hillebrand's specimen

¹ Department of Botany, Duke University, Durham, North Carolina. This study was supported by the National Science Foundation (NSF-Grant 18799). Manuscript received December 24, 1964.

and description, indicating that it differed from the verticillate-leaved "*O. sandwicensis* A. Gray" in possessing opposite leaves and a more densely-flowered inflorescence. Rock (Indigenous Trees Haw. Is.:414, 1913) admitted that he had not encountered the opposite-leaved species but expressed doubt as to its specific dis-

tinctness. The variable Hawaiian populations merit careful appraisals, but this of necessity will require much field study. It is felt that a legitimate name for the Hawaiian species should be made available now. The designation of a neotype can well await the necessary detailed study.

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

ALEXANDER MALAHOFF and G. P. WOOLLARD

*Geologic Implications of Magnetic Surveys Over the
Hawaiian Islands*

HUBERT FRINGS, MABLE FRINGS, and CARL FRINGS

Annotated Bibliography on North Pacific Albatrosses

DONALD W. STRASBURG

Ecology of Four Apogonid Fishes

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Records of Asian and Western Pacific Marine Algae

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New Camallanid Nematode from Hawaii

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Soil Mineralogy on Krasnozems in North Queensland, Australia

NOTES

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Magnetic Surveys Over the Hawaiian Islands and Their Geologic Implications¹

ALEXANDER MALAHOFF and G. P. WOOLLARD

ABSTRACT: A geophysical and geological analysis is made of a total field magnetic survey of the major islands of Hawaii. It is established that the regional distortion of the earth's normal magnetic field due to the topographic mass of the Hawaiian Ridge rising in places to over 30,000 ft above the ocean floor seldom exceeds 150 gammas. On each island, local magnetic anomalies having the form of lenticular and circular dipoles are found. The lenticular dipole anomalies appear to be related to crustal rifts that have been invaded by magmatic material of mantle origin, and the circular dipole anomalies are associated with primary areas of volcanic eruption. Although the inferred crustal rifts have surface geologic expression in some areas, such as the Koolau Mountains on Oahu, for the most part they do not. Furthermore, offshore magnetic data indicate that these features extend beyond the islands and out into the adjacent, deep-water, oceanic area where they can be traced for 100 miles or more. The most pronounced of these features is associated with the ocean floor Molokai Fracture Zone, which magnetically extends across the Hawaiian Ridge without interruption for an unknown distance to the west. The circular dipole anomalies appear to represent the effect of intrusions in volcanic pipes or vents rising from these crustal rifts which strike essentially east-west on the islands of Hawaii, Lanai, Maui, and Molokai, and west northwest-east southeast on Oahu, Kauai, and Niihau. With two exceptions, all of the anomalies indicate normal polarization conformable with the earth's present field.

DURING THE YEAR 1964, the authors carried out the first of a series of planned magnetic surveys over the Hawaiian Ridge and adjacent oceanic area. The area covered extends from the island of Kauai on the north to the island of Hawaii on the south.

In this present paper, the magnetic results are examined on both a qualitative and a quantitative basis as to their relation to the centers of volcanism which built the Hawaiian Ridge and to the primary geologic tectonic trends having surface expression or bathymetric expression on the ocean floor. As will be shown, good correlations exist between the pattern of magnetic anomaly values and the volcanic features of the islands as well as the oceanic rifts having bathymetric expression. In order to minimize the magnetic effects of local changes in geology, soils, and the terrain associated with

mountains such as Mauna Kea (elevation 13,796 ft), the magnetic profiles were flown at least 2,000 ft above the ground surface. Although a complex pattern of magnetic anomalies is obtained because of the low magnetic latitude of Hawaii, the interpretation is straightforward. Depth and size estimations were based on the interpretive procedures of Vacquier et al. (1951) as well as on the basis of magnetic susceptibility-remanence measurements. These results were then compared with those determined from other geophysical measurements and the geologic probability of the anomalous bodies assessed. Finally, the magnetic effects of the derived geologic bodies were computed, using a two-dimensional, high-speed computer program and the derived theoretical profiles compared with those observed. All the profiles used in these comparisons were corrected for terrain. Because the regional magnetic gradient at the low magnetic latitude of Hawaii does not exceed 6 gammas per mile, it

¹ Hawaii Institute of Geophysics, Contribution No. 148. Manuscript received July 20, 1965.

is not necessary to remove the regional magnetic gradient to bring out the relatively large magnetic anomalies ranging from 500 to 2,000 gammas. All anomaly maps were corrected for heading errors which, in general, did not exceed 40 gammas.

METHODS AND MATERIALS

Aircraft and Instrumentation

Most of the observations were obtained by using an Elsec proton magnetometer towed by an aircraft. The sea north of Maui over the buried extension of the Molokai Fracture Zone was surveyed using RV "Teritu" and the U. S. Coast and Geodetic Survey ship "Surveyor." Data for other adjacent marine areas had been surveyed earlier by the Scripps Institution of Oceanography (Arthur D. Raff, personal communication) and the U. S. Naval Oceanographic Office (1962).

The aircraft used for the program was an "E" model of the Stinson L-5 powered by a 190 horsepower Lycoming O-435-1 engine. The magnetic measurements were made with the Elsec magnetometer with a polarization time of 7 seconds. For the speed of the aircraft, flying at approximately 100 miles per hr, this polarization interval permitted a surface sampling interval of 819 ft (250 m). The proton procession signal was registered digitally on a dial readout and recorded by hand in the aircraft.

A total of 18,000 miles was flown in checking out the equipment design, operation, and actual data flights. Access doors opened the right-hand side of the aircraft fuselage, allowing stowage of all equipment needed for the project. An experimental certificate was obtained from the F. A. A. on the aircraft to permit the opening of the side door in flight in order to lower the "bird" which contained the magnetometer sensing head over the side for trailing behind the aircraft. The Elsec magnetometer with its incorporated power supply was placed to the right of the rear seat for operation by the observer. The door was closed after the 100-ft cable was fully extended. The drag induced by the trailing of the bird reduced the airspeed by approximately 5 miles per hr.

The bird was suspended from the aircraft by a braided nylon rope through which passed the

coaxial cable to the magnetometer head. The end of the nylon suspension rope was anchored to a ring welded to the fuselage structure. The bird was designed to be of sufficient size to accommodate the rotation of the sensing head. Prior to each flight, the head was oriented in an east-west direction without regard to the direction of the flight lines. The bird was constructed of a hand lay-up of woven fiberglass cloth and reinforcing mat with polyester resin. The finished laminate was $\frac{1}{8}$ inch thick. Fins made of $\frac{1}{4}$ -inch plywood supported the fiberglass-reinforced tail ring.

Numerous flight tests were conducted to establish the suspension point of the bird for the best flight characteristics. This point was found to be $10\frac{1}{2}$ inches aft of the nose. A spoiler of triangular cross section was added to the top nose surface to decrease the aerodynamic lift of the bird. If the bird was suspended at the incorrect point, an ever-increasing pendulum effect was encountered. The first model of the bird proved unstable. This instability was corrected by lengthening the fins by 4 inches. It was necessary to fly during periods when air turbulence was at a low level or nonexistent in order to obtain valid data. When heavy turbulence was encountered, the bird was immediately retrieved for the safety of the bird and the aircraft. During the project, the bird was flown at speeds up to 100 miles per hr, and on only one occasion during the actual data flights did the bird demonstrate any unusual flight characteristics. This was during a short period of extreme turbulence which occurred over the island of Hawaii near Kawaihae. Severe pitching resulted before the bird could be retrieved into the aircraft.

Navigational checks and positioning were accomplished by a combination of pilotage and dead reckoning. Flight lines were marked on topographical maps of a 1/62,500 scale, with direct observations being made on surface cultural and topographical features during the flights. On over-sea flights, the track, speed, and drift rate were recorded over land and then extrapolated over the seaward portion of the flight line. Horizontal positioning of any flight line of the survey is regarded to be better than the order of 500 ft or 150 m. The over-land flight lines were spread at 1-mile intervals.

Absolute ceiling of the aircraft with all equipment aboard was 15,500 ft. Indicated cruising airspeed of the aircraft with the bird in tow at 10,000 ft was 80 miles per hr, and at 15,000 ft the indicated airspeed was 73 miles per hr. Full power and a high angle of attack were required in order to maintain that altitude. The equipment used proved adequate for all altitudes up to 15,000 ft.

Methods Used in the Interpretation of Magnetic Anomalies

Nearly all the magnetic anomalies observed over the Hawaiian Islands and the neighboring oceanic area can be divided into two groups:

1. Local dipole anomalies related to centers of volcanism marked by surface caldera, volcanic peaks, or geologic evidence defining a former vent area.

2. Elongate, dipole anomalies related to dike complexes, observable, and probable, rift zones in the crust that appear to be occupied by intrusives at depth.

In the study of these anomalies, four factors were evaluated: (1) approximate size and shape of the anomalous geologic body, (2) orientation in the earth's magnetic field at the latitude of Hawaii, (3) depth to the top of the anomalous body, (4) susceptibility contrast and the natural remanent magnetization contrast between the surrounding rocks and the anomalous body.

An approximation to the above parameters can be obtained by utilizing various analytical procedures based on the shape of the anomaly profile for the magnetic latitude. The three parameters can then be further defined through theoretical computations using two- or three-dimensional techniques with machine programming. These results are then matched with those observed.

Most total force magnetic anomalies observed over the Hawaiian Ridge and the surrounding oceanic areas exhibit normally polarized magnetic dipoles which remain as dipoles even after topographic corrections have been applied. These dipoles are of such intensity and wavelength that they can only be interpreted as vertical intrusive rocks intruding into the volcanic domes along elongate rift zones.

As volcanism in the Hawaiian Islands appears in most cases to follow similar structural patterns, a scheme for estimating the horizontal cross-sectional size of the intrusive body, the depth to the top of the body from the level of observation, and the vertical length of the body would be useful for the rapid evaluation of the shapes of such intrusive bodies. The horizontal size of the body may be determined by the inspection of the relationship between theoretical anomaly contours over theoretical bodies, as those computed by Vacquier et al. (1951), and by using this relationship to derive the horizontal size of the body giving rise to the observed magnetic anomaly. Depth to the top of the anomalous body may be readily determined by using "depth indices" such as those in Vacquier et al. (1951). For dipole anomalies over the Hawaiian Islands, the G index was found to be the one giving the most consistent results and less likely to be affected by interference from superposed smaller wavelength dipole anomalies.

As is the case in the Hawaiian Islands, the susceptibility and the natural remanent magnetization contrast between the extrusive and intrusive rocks of the volcanic domes may be obtained from measurements made on rock samples in the laboratory. Theoretical susceptibility contrast may be computed by using the formula

$$K = \frac{\Delta T_m}{\Delta T_c T}$$

where K is the minimum susceptibility contrast (Vacquier et al., 1951); ΔT_c , the total amplitude of the intensity anomaly selected from the appropriate theoretical body, as computed in Vacquier et al.; T , the intensity of the regional magnetic field at the point at which the anomaly is situated; and ΔT_m , the observed amplitude of the actual anomaly.

Having thus determined the above factors, another set of theoretical models, computed for the latitude of the Hawaiian Islands, may be used to determine the total vertical length of the intrusive geologic body.

The amplitude of the magnetic anomaly associated with the geologic body depends on the magnetization of the body, on the length, and on the depth to the top of the body from the

level of observation. A series of theoretical geologic bodies with variable depths to the top of the body and variable length-to-width ratios may be constructed. As the depth to the top of the geologic body increases, the amplitude of the magnetic anomaly profile decreases.

Using arbitrary units for d , the depth to the top of the body, and corresponding arbitrary units for the length and width of the geologic body, a series of theoretical, two-dimensional, vertical geological bodies were constructed and their total force magnetic anomaly profiles computed. Each particular model (Fig. 34A to F) has a set of five of the profiles, computed for $d = 0.5, 1, 2, 5, 10$, and 15 in arbitrary units.

The profiles were calculated using a combined susceptibility-natural remanent magnetization of 10.0×10^{-3} cgs units, a common magnetization contrast, observed from specimens and computed from anomaly profiles, between the intrusive and extrusive basalt rocks of the Hawaiian Islands. The models are assumed to have an infinite horizontal length and a strike parallel to magnetic latitude. The models are magnetized in a regional total force magnetic field of 36,000 gammas, with a dip of 35° N. The total force magnetic profiles are assumed to strike parallel to magnetic longitude, i.e., perpendicular to the strike of the models. In practice it was found that by comparing computed total force magnetic profiles over models that had been computed using two- and three-dimensional techniques, end effect errors, in the case of two-dimensional assumptions, are likely to be less than 10% if the geologic body has in horizontal section a width of one unit and a length of four units.

The total force magnetic anomaly profiles were computed by using machine programming in integrating the effects of horizontal and vertical magnetic fields of volume elements over the cross sections of the geologic models (Heirtzler et al., 1962).

By comparing observed total force magnetic anomaly profiles with those computed in Figure 34A to F, the figures become useful as a means of rapidly determining the vertical length of the highly magnetized, vertically or near-vertically dipping intrusives intruded within the Hawaiian volcanoes of the Hawaiian Ridge, or within elongate seamounts or rift zones of the ocean

floor, in the magnetic latitude where the magnetic dip is between 30° and 40° . Similar relationships would also hold true for the above-mentioned geologic features within the Southern Hemisphere latitudes where the magnetic dip is also from 30° to 40° , though the anomaly dipoles would be reversed in sign.

The curves in the figure may also be used in aeromagnetic surveys to measure the magnetic sensitivity with elevation. For instance, if zones of magnetization 1 km in width are to be examined at an elevation of 3 km, extremely sensitive instrument techniques would have to be used in order to determine whether the zones of magnetization are 40 km in vertical length (Fig. 34E). On the other hand, too low a flight elevation will record anomalies that are great in amplitude with steep gradients—frequent crowding of anomalies—which may lead to difficulties in sorting.

For the equatorial latitudes at least, the best flight elevation with respect to the wavelength of the geologic body to be examined is that with a ratio of 1:1 (Fig. 34D). That is to say, at a flight elevation of 2 km, reasonable total amplitudes of 700 gammas peak-to-peak to 120 gammas peak-to-peak for the anomalies can be expected, depending upon the vertical length of the magnetized body. At this ratio, reasonable estimates of the vertical lengths of the magnetized bodies can also be made, because the total wavelengths of the anomalies caused by relatively short geologic bodies are readily distinguishable from those caused by relatively long geologic bodies.

This procedure for determining the lengths of intrusive magnetized bodies and for selecting appropriate aeromagnetic flight elevations may be used at any magnetic latitude, providing an appropriate selection of models is computed for that latitude range.

RESULTS, DISCUSSION, AND CONCLUSIONS

Problems in Magnetic Surveying Over Magnetic Terrain

The primary advantage of an aeromagnetic survey method over those of ground surveys is the greater rate and density of coverage that can be achieved. An additional advantage is that the effect of changes in surficial geology and terrain

is not only minimized, but the terrain corrections are simplified. In ground surveying methods, such as those described by Nettleton (1940), terrain corrections are not considered because only relations found in petroleum provinces are treated. In such areas, the sedimentary rocks encountered at the surface are relatively non-magnetic as compared with the buried crystalline rock complex at depth, and the terrain effect is negligible. Ground magnetic surveys in such areas, therefore, define geologic boundaries beneath the sediments in the crystalline rock complex.

Surveying over a surficial magnetic rock surface presents an entirely different problem. In such areas, a magnetic dipole is induced over each topographic rise as well as subsurface bodies having an abnormal magnetic susceptibility. Because the magnetic intensities of any two-pole magnetic body vary inversely as the square of the distance between the sensing head of the magnetometer and each of the induced poles on the geologic or topographic body creating the anomaly, near-ground magnetic surveys over highly magnetic country rock, such as basalt, reflect local terrain irregularities as well as the effect of buried geologic bodies. Which effect will be dominant depends upon the relative susceptibility contrast associated with each body, the size of the respective bodies, their geometry, orientation in the earth's field, and the distance from the magnetometer sensing head to each body. To illustrate this relationship, the apparent susceptibility contrasts between air and normal basalt is of the order of 15.0×10^{-3} cgs units, which is similar to the contrast between normal basalt and intrusive gabbroic dike rock. If all other factors are equal, but the distance between the sensing head and a local basaltic terrain feature (such as the wall of a caldera) is of the order of 20 ft, and the distance between the sensing head and the top of an intrusive mass in the underlying volcanic feeder pipe is of the order of thousands of feet, it is obvious that the terrain effect will be dominant. To assess the magnetic effect of basaltic terrain in Hawaii, a total force ground magnetic survey as well as an airborne survey was carried out across the crater of Kilauea Iki on the island of Hawaii.

Kilauea Iki is a small side crater merging

with Kilauea Crater along the northeastern portion of the latter. The floor of the small crater lies 650 ft below the rim. The total magnetic intensity, as observed with the polarizing head 4 ft above ground level, varied from a reading of 39,400 gammas at the rim of the caldera to a reading of 34,300 gammas at the floor of the caldera. This change would normally be interpreted as indicating a magnetic anomaly of $-5,100$ gammas due to anomalous geology located within the confines of the Kilauea Iki crater. However, if the aeromagnetic anomaly above Kilauea Iki is examined, the maximum residual anomaly that can be assigned to an anomalous body within the crater is only 60 gammas. Also, it was noted that, if a magnetic reading is taken on basaltic terrain at 5 ft above ground level, a difference of up to 300 gammas can be obtained from the effects of local irregularities in terrain. Because of this pronounced ground-level terrain effect and the occurrence of highly ferromagnetic secondary minerals in basaltic soils, no surface magnetic surveys were attempted for the study of subsurface geologic structure. All observations were made using an airborne system.

The flight elevations over the islands varied between 15,000 ft above sea level for flights above the peaks of Mauna Loa and Mauna Kea on the island of Hawaii to 8,000–10,000 ft for the remaining islands. These elevations were chosen on the basis of theoretical studies of the magnetic effects to be expected for topography. At a flight elevation of 10,000 ft, the magnetic effect to be expected for an 8,000-ft peak built of material with a magnetic susceptibility of 1.0×10^{-3} cgs units and a natural remanent magnetization of 10.0×10^{-3} cgs units should be of the order of ± 100 gammas. It was on the basis of both theoretical and actual profiles across the topographic features of Maui, Molokai, and Oahu that a standard flight elevation of 8,000–10,000 ft above sea level was selected for use everywhere except where this elevation would not permit clearance of the land surface by at least 2,000 ft.

Comparison of Ship and Airborne Magnetic Survey Data at Sea

The total force magnetic intensity survey results obtained with the airborne magnetometer

required only a correction for the heading error resulting from towing the polarizing head in a north-south direction 100 ft behind the plane. The average heading error varied from 30 to 40 gammas. Because the normal magnetic field gradient was low, no significant error would have been introduced if this effect had been neglected.

The total force magnetic field out to 150 miles north of Maui was surveyed by the U. S. Coast and Geodetic Survey ship "Surveyor," whereas the remainder of the offshore areas adjacent to the islands were surveyed using the University of Hawaii RV "Teritu." However, aeromagnetic profiles were also taken over the sea tracks of the "Surveyor" out to 50 miles north of Maui. Although the aircraft was flown at 8,000 ft above sea level and the ship observations were made a few feet below sea level, no significant differences in values were observed between the airborne and seaborne data. This lack of difference in values can be attributed to the great depth of the anomalous geologic bodies lying below the ocean floor which cause ocean magnetic anomalies.

Possible Origin of Hawaiian Magnetic Anomalies

Magnetic anomalies result from changes in the magnetic characteristics of rock masses which, in general, can be related to the percentage of magnetite and ilmenite present. As these two minerals are present to some extent in most igneous rocks, the natural thing to expect in the magnetic study of an oceanic archipelago of volcanic origin, such as the Hawaiian Islands, is a composite anomaly pattern. The basic component would be that portion which can be related directly to the size and geometry of the volcanic mass rising from the sea floor and the strength and inclination of the earth's magnetic field, and on this would be superimposed the effect of local variations in types of lava present and intrusions within the volcanic pile.

Even a casual inspection of the regional magnetic map (Fig. 1) shows that the island mass effect of the Hawaiian Islands is of such secondary importance as to be lost in the overriding magnetic effects originating from other geologic causes. This empirical observation is further substantiated by quantitative calculation,

which indicates that only about a 60-gamma effect is to be expected for the island mass. Similarly, local variations in the lavas present do not appear to be too significant in terms of changes in the anomaly pattern. Although there may be petrologic significance in the somewhat smaller magnitude anomalies observed on the island of Hawaii as compared with other, older islands, this could also be the result of higher temperatures at depth in this island, which is the only one now characterized by active volcanism. Probable areas of abyssal intrusion defined by either surface fracture systems or volcanic centers of eruption are associated everywhere with the magnetic anomalies which occur mostly as dipole pairs. It is significant, though, that only primary central vent areas and rift (fracture) zones that were the source of the bulk of the volcanic rocks forming the islands are marked by magnetic anomalies. Secondary centers of eruption, such as Diamond Head on Oahu, are not defined magnetically. In connection with rift zone type of anomalies, Figure 1 shows that most of the rift zone type anomalies do not terminate at the physical boundaries of the islands on which they occur. Some extend for considerable distances into the adjacent oceanic area. This suggests that the rift zone type anomalies may well be independent of the geology of the islands and are related to intrusions at depth in crustal fractures. Along these rifts, and locally at the intersections of crosscutting crustal fractures, magma penetrated to the ocean floor to initiate a series of seamounts that developed into the Hawaiian Islands. Because each locus of magmatic intrusion (whether now defined geologically by a major volcanic mountain peak, such as Mauna Kea on Hawaii, a submerged seamount, a deeply dissected vent area recognizable only through its associated dike complex and boundary faults, such as the ancient Waianae caldera and the present day Koolau range on Oahu or the Molokai Fracture Zone on the ocean floor) requires a similar theoretical contrast in magnetic susceptibility, it is probable that the controlling lithology at depth is much the same in each case and represents some differentiate of what originally was probably mantle material. This conclusion is based, in part, on depth analysis as the source of the magnetic anomalies as well as the seismic



FIG. 1. Total force magnetic intensity map of the Hawaiian Swell, Hawaii to Oahu. Contour interval at 100 gammas. (After Malahoff and Woollard, 1965.)

refraction measurements which indicate the rift zone type anomalies originate from depths ranging from 4–10 km below sea level. The failure to obtain magnetic anomalies over the late-stage centers of volcanic activity, such as Diamond Head and Koko Head on Oahu which were centers of alkalic basalt extrusion, probably lies not so much in the difference in the mineralogic constituents of the extruded lavas, but rather in the difference in susceptibility contrast between the rock at depth representing the source magma and the enclosing rock. Whereas the primary intrusions appear to have had their magma source in the mantle and were emplaced in the crust, the late-stage intrusions could well have been derived from shallow magma chambers that developed (Eaton, 1962) within the volcanic pile itself. Thus, the composition of the magma and its equivalent rock magnetic susceptibility could be essentially the same as that of the primary enclosing tholeiitic basalt, and the alkalic basalt would be the result of *in situ* differentiation through the gravity separation of early formed olivine, as suggested by Macdonald et al. (1960).

Under these conditions there would be no contrast in magnetic susceptibility either at the surface over the vent or at the depth of the magma chamber, since the bulk of the available iron would be in the form of nonmagnetic silicates rather than oxides. Although these observations do not identify the exact lithologic character of the rock material causing the observed anomalies, it does appear to be an intrusive which contains a higher percentage of magnetite and possibly ilmenite than does the enclosing crustal rock. Because the associated gravity anomalies all indicate that these intrusives must also have a density of 3.2 gm/cc, it is probably very similar to peridotite. However, until one or more anomalous areas, such as the Koolau caldera on Oahu, are drilled, no real answer can be given to this problem.

Magnetic Properties of Rocks of the Hawaiian Islands Used in the Reduction of Magnetic Data

As susceptibility and the natural remanent magnetization of rocks are essential factors in the interpretation of the total force magnetic anomalies, it might be well to review the data for the Hawaiian Islands. Studies of this nature

on the Hawaiian rocks have been carried out by Doell and Cox (1963), Decker (1963), and Tarling (1963) as well as by the senior author of this paper. The results of all these determinations are summarized in Table 1.

As the table shows, there are two groups within the extrusive basaltic rocks that appear to have greatly differing susceptibilities and intensities of natural remanent magnetization. The first group, those having low magnetic susceptibilities, are predominantly olivine-rich rocks, in which olivine makes up more than 15% of the total weight of the rock sample. Rocks in this group include those from Hualalai Volcano on the island of Hawaii, which have susceptibilities that average 0.41×10^{-3} cgs units and intensities of remanent magnetization that range from 0.5 to 5.0×10^{-3} cgs units, and samples of garnet peridotite from Salt Lake Crater on Oahu, which range in susceptibility from 0.4 to 0.5×10^{-3} cgs units and have an intensity of remanent magnetization which averages between 1.0 and 2.0×10^{-3} cgs units.

In the second group, those having a high magnetic susceptibility, are the olivine-poor lavas, such as those found on the island of Hawaii. These olivine-poor lavas have an average susceptibility of 2.5×10^{-3} cgs units and natural remanent magnetization of 10.0×10^{-3} cgs units.

Similarly, intrusive rocks show extensive variations in magnetic properties. One dike rock sample collected on East Maui had a susceptibility of 6.8×10^{-3} cgs units and a natural remanent magnetization of approximately 100×10^{-3} cgs units. On the other hand, fine-grained dike rocks collected near the Iao Needle, West Maui, had an average susceptibility of only 0.12×10^{-3} cgs units and a remanence of 3.0×10^{-3} cgs units. These low values of magnetic properties of West Maui intrusive rocks could account perhaps for the reversed dipole effects in the magnetic field observed over West Maui. However, most of the intrusive rocks sampled in the Hawaiian Islands have intensities of remanent magnetization that are, on the average, higher by 5×10^{-3} to 10×10^{-3} cgs units, and susceptibilities that are higher by 2×10^{-3} cgs units than the basaltic lavas which they intrude.

Altogether, 40 samples of basalt were col-

TABLE 1

AVERAGE VALUES¹ OF SUSCEPTIBILITY (μ) AND NATURAL REMANENT MAGNETIZATION FOR ROCKS OF THE HAWAIIAN ISLANDS

FORMATION	NRM (Tarling, 1963)	μ	NRM ² (Authors)	μ	NRM (Decker, 1963)	μ
Hawaii (tholeiite)			11.0	3.2	10.0	1.0
Hawaii (olivine-rich basalt)			5.0	0.5		
Hana (E. Maui)	17.31	4.63	—	—		
Kula (E. Maui)	137.30	13.28	100.0	5.0		
Honomanu (E. Maui)	0.96	2.66	1.0	2.5		
Honolua intrusive rock			20.0	2.8		
Honolua (W. Maui)	14.34	2.74	15.0	2.7		
Wailuku intrusive rock			1.0	0.5		
Wailuku (W. Maui)	8.19	2.01	10.0	2.8		
Lanai	5.88	0.92				
East Molokai	19.43	2.13				
West Molokai	13.22	1.16				
Koolau dike rock (Oahu 1) ³			20.0	3.2		
Koolau dike rock (Oahu 2) ⁴			2.0	0.5		
Koolau (Oahu)	3.09	1.83	5.0	1.8		
Waianae (Oahu)	2.67	2.19	—	—		
Honolulu peridotite	—	—				0.4
Honolulu (Oahu)	4.78	3.92	3.0	3.2		
Koloa (Kauai)	6.45	1.24	5.0	2.1		
Napali (Kauai)	4.21	1.01	5.0	2.0		
Niihau	—	—	—	—		

¹ Values in cgs units by 10^{-3} .² As determined with an astatic magnetometer.³ Dike rock collected along Pali Highway (Oahu 1).⁴ Dike rock collected from Keolu Hills quarry (Oahu 2).

lected from the island of Hawaii, representing both tholeiitic and alkalic basalts; 20 samples were collected from the island of Maui, representing both intrusive and extrusive rocks; 30 samples were collected on Oahu, and 10 on Kauai. All samples were collected from unweathered outcrops and were oriented in the field. Susceptibilities of the rock samples were measured by using cores and a susceptibility bridge. The rock cores were bored in a direction parallel to the vector of the earth's present magnetic field in Hawaii, and intensities and direction of polarization (whether normal or reversed) were measured with the aid of a simple astatic magnetometer.

Because the islands of Hawaii have been formed by the extrusions of numerous stratigraphically thin basaltic flows, whose magnetic properties appear to vary from flow to flow,

the susceptibilities used in topographic reductions and anomaly computations were averaged out for each individual volcano. The collection pattern followed, therefore, was one which would give samples representing as large a vertical section through a given volcano as possible.

The susceptibilities for rocks on the island of Hawaii for all the volcanoes except Hualalai average $2.3 \times 10^{-3} \pm 1.0 \times 10^{-3}$ cgs units. However, 80% of the rock samples have a value of $2.2 \times 10^{-3} \pm 0.5 \times 10^{-3}$ cgs units. The intensities of remanent magnetization average 11×10^{-3} cgs units. As indicated earlier, the olivine-rich basalts collected from Hualalai Volcano had low susceptibilities of the order of $0.4 \times 10^{-3} \pm 0.2 \times 10^{-3}$ cgs units. The values adopted for all computations on Hawaii except Hualalai Volcano were 2.2×10^{-3} cgs

units for susceptibility and 11×10^{-3} cgs units for natural remanent magnetization.

For purposes of computation, the extrusive rocks on the islands of Maui and Kahoolawe were divided into two groups: those of West Maui and those of East Maui (the latter including Kahoolawe). However, no rock samples were actually collected on Kahoolawe, because it is a bombing range and a closed area. In assuming the same susceptibilities and intensities of natural remanent magnetization for East Maui and Kahoolawe, no error is likely, for, as seen from inspection of the total intensity magnetic map of Maui and Kahoolawe (Fig. 2), it appears that both Haleakala Volcano and Kahoolawe originated from extrusions from the same "primary" rift zone.

On East Maui, the bulk of the lavas is represented by the Honomanu basalts, which have an unusually low remanence value which averages 1.0×10^{-3} cgs units with an average susceptibility of 2.6×10^{-3} cgs units. Rocks of Kula series, on the other hand, which have a maximum thickness of 2,000 ft at the summit of Haleakala, have an unusually high n.r.m. (natural remanent magnetization) of 137.3×10^{-3} cgs units. Because the data available are too sparse to determine what is a true representative n.r.m.-susceptibility value for the bulk of the rocks forming East Maui, the writers were forced to compromise and use an average value for all the rocks sampled in East Maui. Therefore, using Tarling's values (Table 1), as well as the writers' values, a mean natural remanent magnetization of 15.0×10^{-3} cgs units was employed in computing the topographic effects on East Maui and Kahoolawe.

Similarly, an average value using Tarling's and the writers' values of 12.1×10^{-3} cgs units for the n.r.m. and 2.7×10^{-3} cgs units for susceptibility was employed for the topographic reduction over West Maui.

Inasmuch as the writers did not collect any samples on Molokai and Lanai, Tarling's values were used in the magnetic computations involving these islands. An n.r.m. of 5.88×10^{-3} cgs units and a susceptibility of 0.92×10^{-3} cgs units were used for the island of Lanai. An n.r.m. of 19.43×10^{-3} and a susceptibility of 2.13×10^{-3} cgs units were used for East Molokai, and an n.r.m. of 13.22×10^{-3} cgs

units and a susceptibility of 1.16×10^{-3} cgs units were used for West Molokai.

The topographic effects of the Waianae and Koolau volcanic series on the island of Oahu were reduced using the following values. An n.r.m. of 2.67×10^{-3} cgs units and a susceptibility of 2.19×10^{-3} cgs units based on Tarling's measurements were used for the topography associated with the Waianae volcanic series. An n.r.m. of 4.47×10^{-3} cgs units and a susceptibility of 2.68×10^{-3} cgs units were used for the topography associated with the Koolau volcanic series. However, intrusive rocks sampled by the writers in the Koolau caldera showed considerable variation in values. Specimens of fine-grained, dark, magnetite-rich intrusive rocks collected near the periphery of the caldera had an n.r.m. of approximately 20.0×10^{-3} cgs units and a susceptibility of 3.9×10^{-3} cgs units. On the other hand, fine-grained, dense intrusive rocks, rich in pyrite, collected near the center of the caldera had an approximate n.r.m. of 1.0×10^{-3} cgs units and a susceptibility of 0.5×10^{-3} cgs units. Because of the scarcity of suitable outcrops, it is not known which of these intrusive-rock suites is representative of the bulk of intrusive rocks at depth. However, as both of the suites of intrusive rocks sampled are normally polarized and the Koolau magnetic anomaly (Fig. 3) is inversely polarized, a possible explanation for the inverse polarized anomaly on the basis of the data available may be that the magnetic anomaly results from rocks having lower susceptibility and n.r.m. value than the surrounding basalts, present at depths within the Koolau caldera.

The magnetic properties of rocks on Kauai were averaged and only one set of values was used because there appears to be little difference in values between the Koloa basalts and the Napali basalts. For the topographic reductions on Kauai as well as on Niihau an n.r.m. value of 5.14×10^{-3} cgs units was used.

In order to solve many of the problems stated in this paper concerning the gross differences observed in the magnetic properties of rocks collected in the Hawaiian Islands, a thorough program of sampling both intrusive as well as extrusive rocks will be necessary. Sampling of both bathymetric and topographic features over the Hawaiian Ridge will be necessary also. Be-

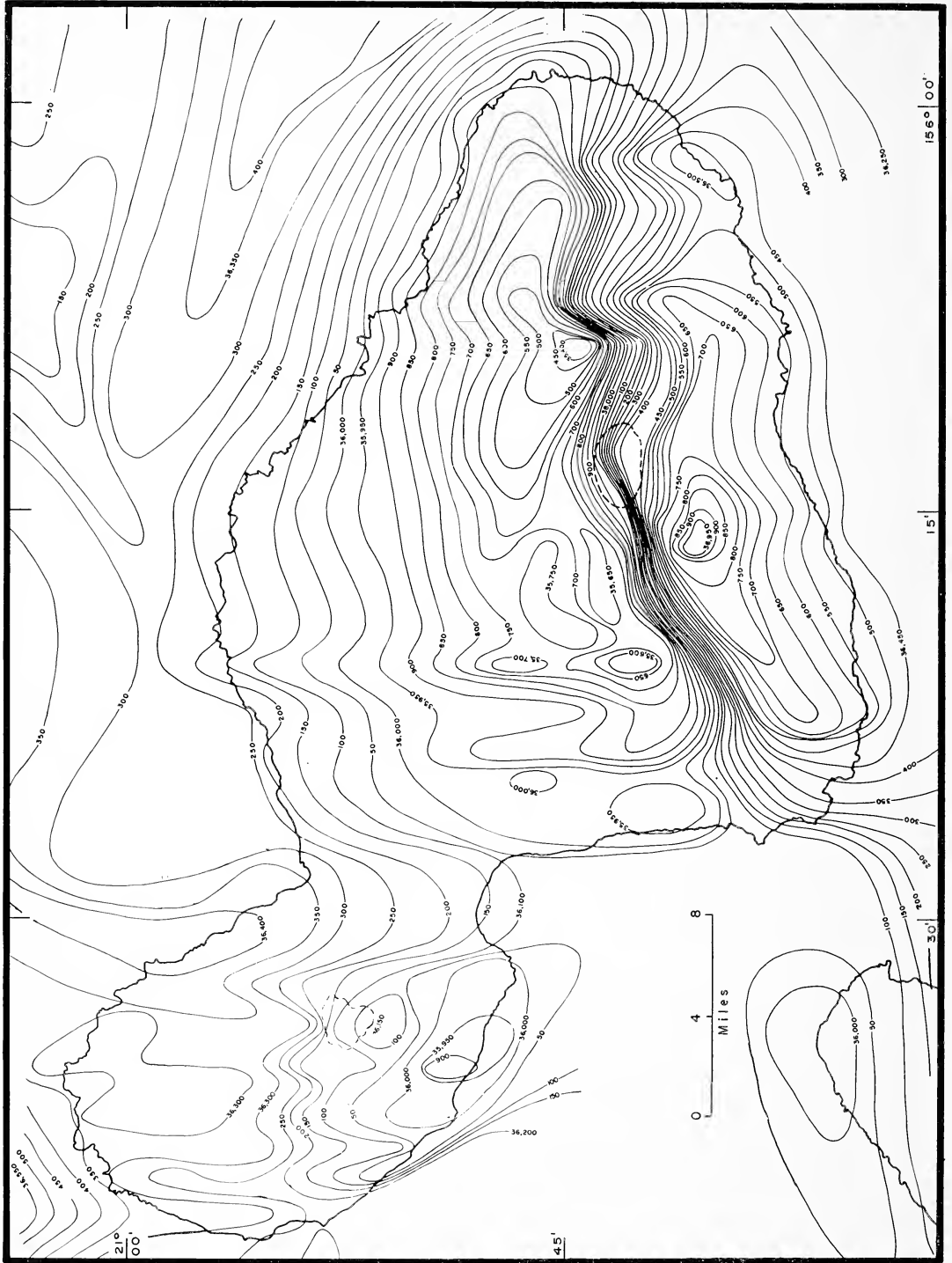


FIG. 2. Total force magnetic map of the island of Maui, based on aeromagnetic profiles flown at 12,000 ft. Contour interval at 50 gammas.

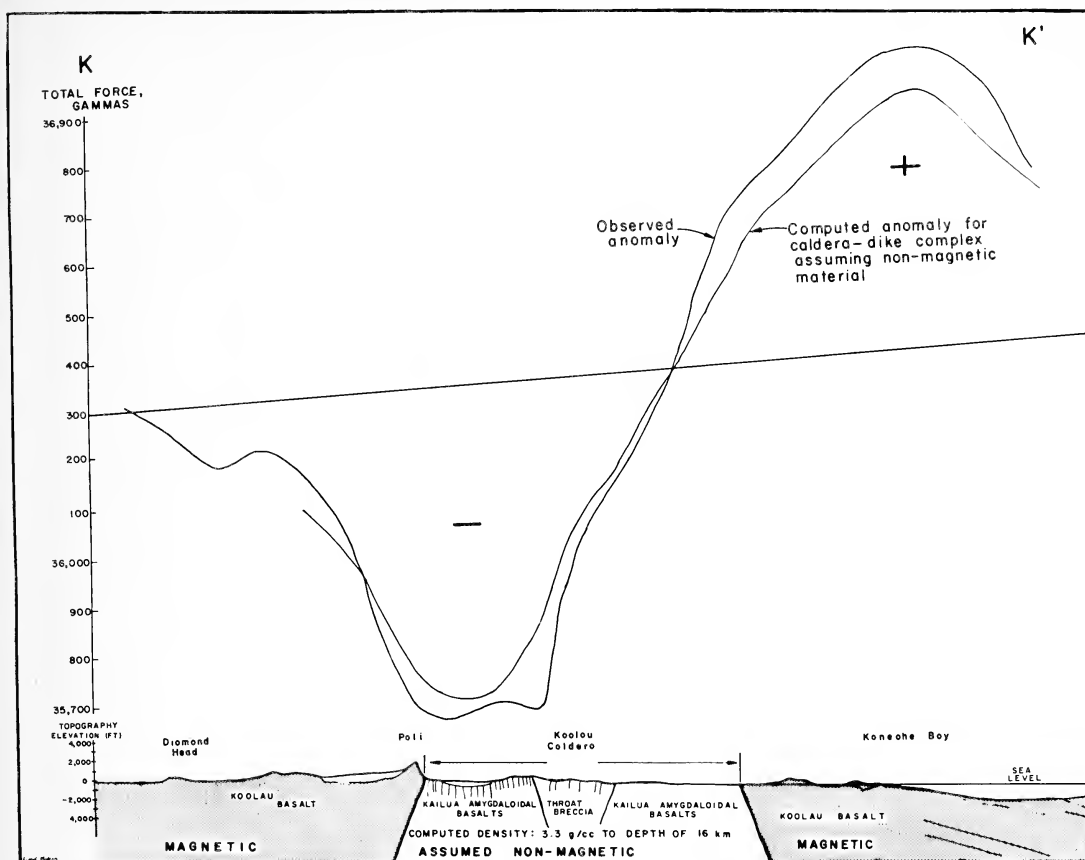


FIG. 3. Magnetic profile along line K-K' (see Fig. 29), Diamond Head-Kaneohe Bay, across the Koolau caldera, island of Oahu.

cause of the lack of suitable samples, the writers adopted an average value of n.r.m. of 10.0×10^{-3} cgs units and a susceptibility of 1.0×10^{-3} cgs units for the basaltic rocks forming bathymetric features.

Although it can be argued that, because all of the Hawaiian Islands are composed predominantly of tholeiite, average magnetic values could have been used also for all of the islands, rather than somewhat different values for each island, such a procedure cannot be justified when the data in hand indicate there are real differences in average values for each island. Even though the lithology may be identical, this does not guarantee that the n.r.m. values, which are related to the strength and direction of the earth's field at the time of eruption, will be the same, inasmuch as it is known that the earth's field is subject to secular change.

The Magnetic Field Over Offshore Areas

The Hawaiian Islands were the first portions of the Hawaiian Ridge to be surveyed in this investigation. Because of the apparent complexity of the magnetic field observed over the islands, and the lack of knowledge of the nature of the anomaly-free regional magnetic field, a companion marine magnetic survey was essential. Although both the U. S. Navy Oceanographic Office of the Scripps Institution of Oceanography as well as the U. S. Coast and Geodetic Survey had made magnetic surveys in the region, none of these covered the essential area adjacent to the islands. The first measurements related to the present study were carried out to sufficient distance north of Maui to avoid probable magnetic anomalies over the extension of the Molokai Fracture Zone, which the Scripps Institution of Oceanography measurements

(Arthur D. Raff, personal communication) had shown to be magnetically disturbed. These measurements were carried out on the "Surveyor."

The total magnetic intensity map of the area studied is shown in Figure 4. This map shows a striking convergence of anomalies and steep magnetic gradients immediately north of Maui. Farther north, beyond the nearshore anomalies which are associated with elements of the Molokai Fracture Zone, and north of latitude $21^{\circ}41'$ the magnetic field over the Hawaiian Rise is smooth, with a uniform gradient of 6 gammas per degree of latitude. Although magnetic anomalies are observed north of $21^{\circ}40'$ which are of the same wavelength (20 km or greater) as those observed south of this latitude, the amplitudes of these anomalies to the north do not exceed 100 gammas.

Of local significance in this survey are the two distinct dipole anomalies associated with the Molokai Fracture Zone north of Maui. One lies 20 miles north of Maui, where a 1,300-gamma peak-to-peak anomaly occurs. The other lies 20 miles northwest of Maui, where a 1,200-gamma peak-to-peak anomaly occurs.

By using depth and susceptibility contrast estimations coupled with two-dimensional model studies, the following geologic analyses were determined. The dipole anomaly centered at $156^{\circ}15'W$ and $21^{\circ}10'N$, and here named the "Hawaiian Deep magnetic anomaly," appears to be caused by an intrusive body some 25 km wide and 65 km long, striking approximately east-west. The top of the anomalous body lies at a depth of about 8.5 km below sea level and it appears to extend vertically downward to a depth of 17.5 km. The rock associated with this body appears to have a susceptibility that is greater by 18.0×10^{-3} cgs units than that of the surrounding crustal rock. As indicated, geographically this anomaly is situated directly above the crustal downwarp and bathymetric low termed the Hawaiian Deep. It is also situated directly above a small bathymetric feature within the Hawaiian Deep that varies from 10–20 km in width and in height from 600–1,600 m (see Figs. 5 and 6). It is significant that the area of the shallow "Moho" depth of 5.8–7 km recorded by Shor and Pollard (1964) and Western Geophysical Company (unpublished)

lies on the western end of this anomaly and over the center of the disturbing body as defined by the point of inflection of the magnetic anomaly (Fig. 7). Thus, there is a reasonable argument that the anomalous Moho depth and the magnetic anomaly are related to the same cause. Considering the uncertainty in the depth analysis of magnetic anomalies, and the fact that the induced upper pole may not correspond to the actual upper surface of the body, there is also reasonable agreement with the seismic depth of 5.8–7 km and the magnetic depth determination of 8.5 km. As the anomaly is normally polarized, and the combined magnetic and seismic data show that the disturbing rock mass is not only more magnetic than the surrounding crustal rock but also extends well below normal mantle depths (12 km) and has a normal mantle velocity, it must represent an intrusion of mantle material into the crust and not represent a crustal displacement as postulated by Shor and Pollard.

Similarly, the normally polarized magnetic anomaly which is centered on $156^{\circ}10'W$ and $21^{\circ}05'N$ appears to be related to an intrusion that is 35 km long and 24 km wide. This anomalous region strikes southwest and abuts against the island of Maui. Its top appears to be located at about 9.0 km below sea level. The rocks causing the anomaly appear to have a greater than the surrounding rocks by about 11.0×10^{-3} cgs units.

As indicated earlier, no significant magnetic anomalies are observed, or are to be expected, in association with the Hawaiian Ridge itself. Similarly, the magnetic effect of bathymetric features at a depth of 13,000–18,000 ft below the plane of observation is observed to be negligible. All the observed magnetic anomalies appear to have resulted from intrusive rock sources.

The Regional and Residual Magnetic Field North of Maui

The observed regional magnetic gradient north of Maui, as deduced from Figure 4, is 6 gammas per minute of latitude; and that determined south of the Hawaiian Islands, from data taken by the U. S. Naval Oceanographic Office (1962), is 5 gammas per minute of latitude. Removal of the regional magnetic field from the total intensity magnetic field of the ocean

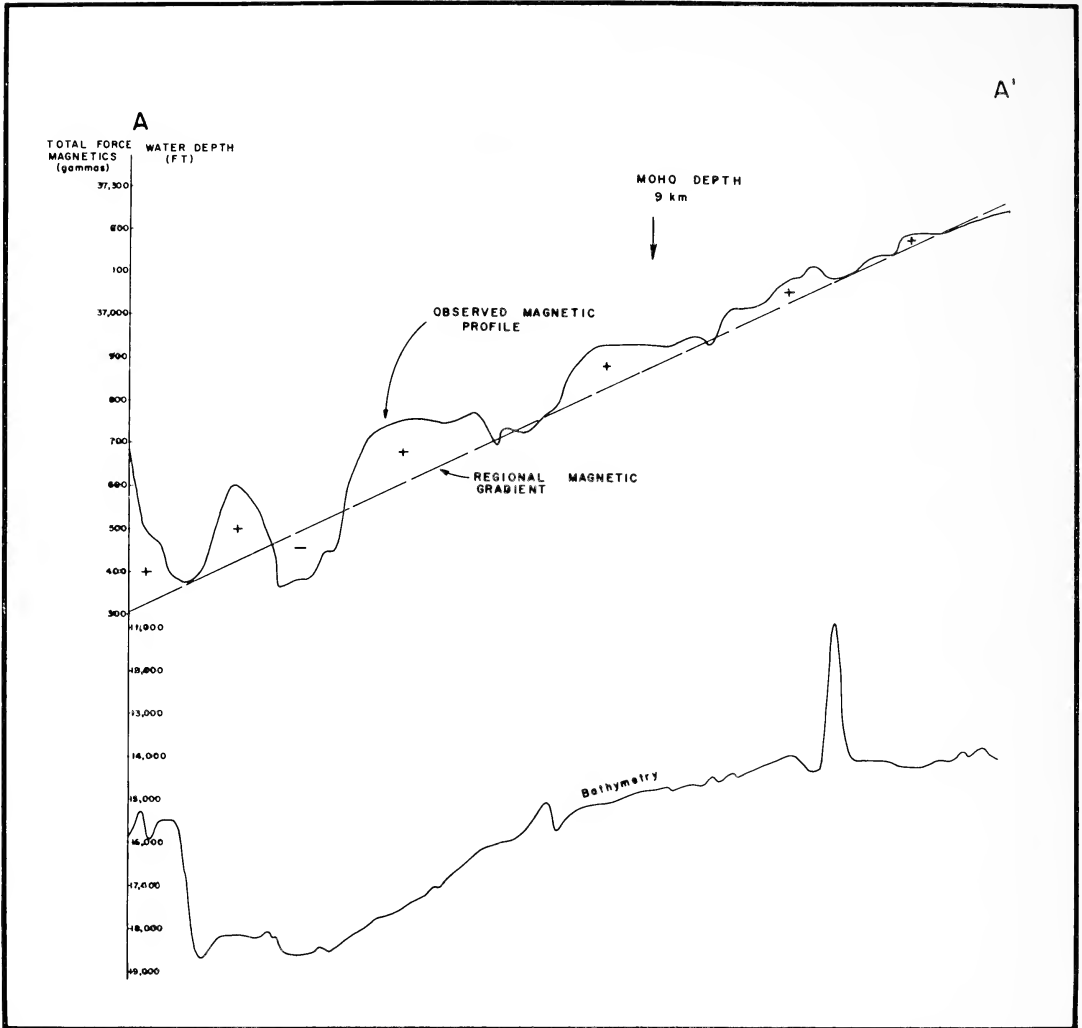


FIG. 5. Magnetic profile along line A-A' (see Fig. 4) north of the island of Maui.

area north of Maui does not change any characteristics of the major anomalies and only brings out low-amplitude, large-wavelength (10–20 km) anomalies, as shown in Figure 8.

Because the gradient of the regional magnetic field over the Hawaiian Islands is low in comparison with the large amplitude of observed magnetic anomalies, no attempt was made to remove the regional magnetic field from the other areas studied.

The Molokai Fracture Zone

Menard (1964) shows that the Molokai Fracture Zone extends from the Baja California Seamount Province to the edge of the Hawaiian

Deep, where the bathymetric expression of the fracture zone disappears. On the basis of bathymetric data alone, this marks the terminus of the Molokai Fracture Zone. However, as will be shown, magnetic data suggest that it continues across the Hawaiian Ridge for a presently undetermined distance westward.

By combining magnetic data taken by the U. S. Naval Oceanographic Office (1962), the University of Hawaii, and the Scripps Oceanographic Institute (Arthur D. Raff, unpublished), it is possible to relate magnetic anomalies to this and other prominent bathymetric features. As seen from Figure 9, the magnetic anomalies, as well as bathymetric features as-

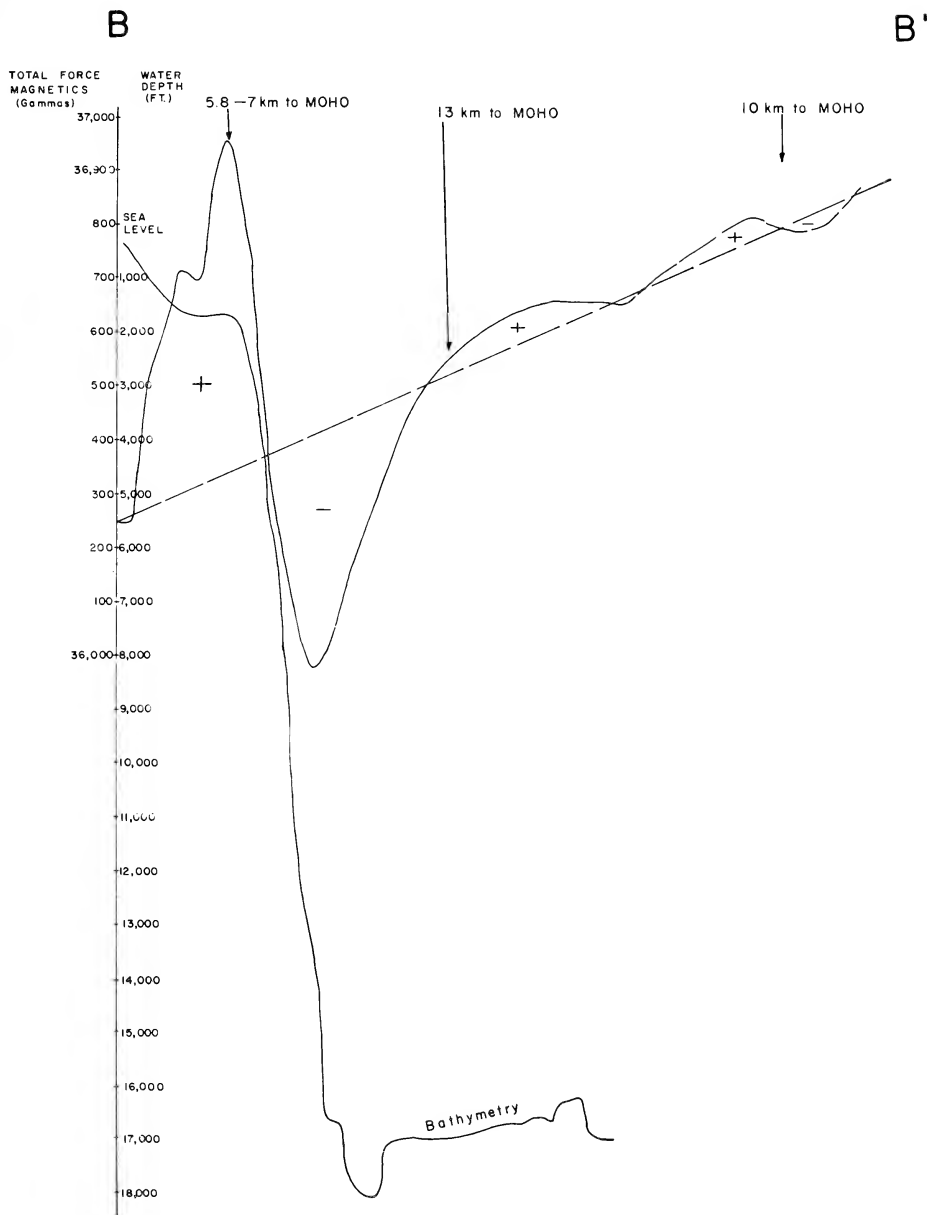


FIG. 6. Magnetic profile along line B-B' (see Fig. 4) north of the island of Maui.

sociated with the Molokai Fracture Zone, occur as elongated parallel bands. It is also noted that the magnetic anomalies observed along the bathymetric expression of the Molokai Fracture Zone have a distinctive high amplitude. Because the topographic effect of the associated bathymetry cannot alone explain the anomalies, there must be associated intrusive rocks having a high magnetic susceptibility. Although it is not

known whether these actually crop out, a depth analysis of the anomalies suggests that they do not, and that relations are similar to those defined seismically and magnetically north of Maui. In other words, it appears that the anomalies are caused by intrusions into crustal fractures developed by lateral faulting. Therefore, it is not surprising that, although the bathymetric expression of the Molokai Fracture Zone ceases

near the edge of the Hawaiian Deep, the associated magnetic anomalies continue westward without interruption along the strike of the Molokai Fracture Zone. However, it is to be noted that there are some notable changes where this trend intersects that of the Hawaiian Ridge. North of Maui, as seen from Figure 4, the "Hawaiian Deep magnetic anomaly" bifurcates into two distinct anomaly trends. One trend crosses the island of Molokai and continues to strike in an east northeast–west southwest direction for at least another 600 km without any change in strike direction. The second trend strikes to the northwest, to merge into the anomaly defining the Koolau Primary Rift Zone of Oahu (Fig. 10).

Two local high amplitude magnetic anomaly dipoles are superimposed on the Koolau Primary Rift Zone anomaly. One anomaly (1,400 gammas peak-to-peak) is located over the Koolau caldera on Oahu. The other anomaly (1,600 gammas peak-to-peak) is located in the Kaiwi Channel and has no known geologic counter-

part. Over the northwestern portion of Oahu, the Koolau Rift Zone anomaly merges with the Waianae Primary Rift Zone anomaly on the leeward side of Oahu to form a single anomaly trend striking in a direction parallel to the strike of the axis of the Hawaiian Ridge. As the southern end of the Waianae Primary Rift Zone anomaly terminates against the west southwest strike of the Molokai Fracture Zone anomaly belt, it appears to have been broken by translational movement along the latter. This is the only notable instance of direct discordance between the strike of the Hawaiian Ridge-oriented magnetic anomalies and the magnetic anomalies oriented parallel to the Molokai Fracture Zone.

If the elongate primary magnetic anomalies represent crustal fractures invaded by mantle material, Figure 10 defines the "rift" zones. These were constructed along the inflection zones of the elongate magnetic dipole anomalies as marking the geographic location of the source of the anomalies. As will be seen, primary volcanic vents are marked by intense local dipole

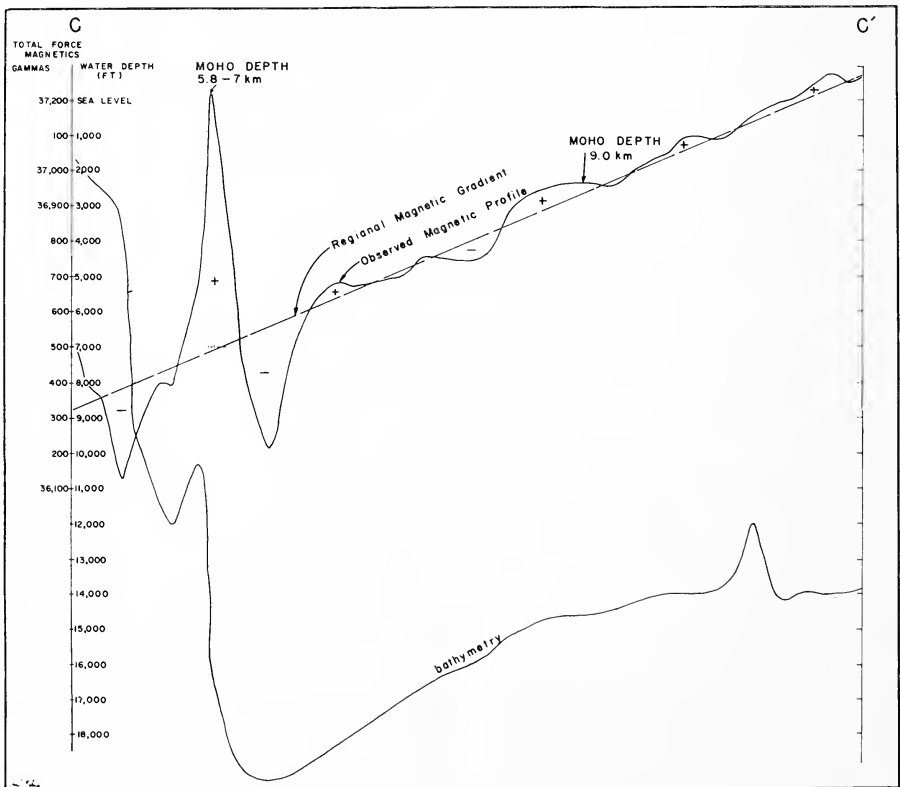


FIG. 7. Magnetic profile along line C-C' (see Fig. 4) north of the island of Maui.

anomalies located, on the islands at least, along the axes of rifts defined by the primary anomaly trends.

Inasmuch as the majority of the primary anomaly trends and rift zones defined south of the island of Oahu appear to strike parallel to

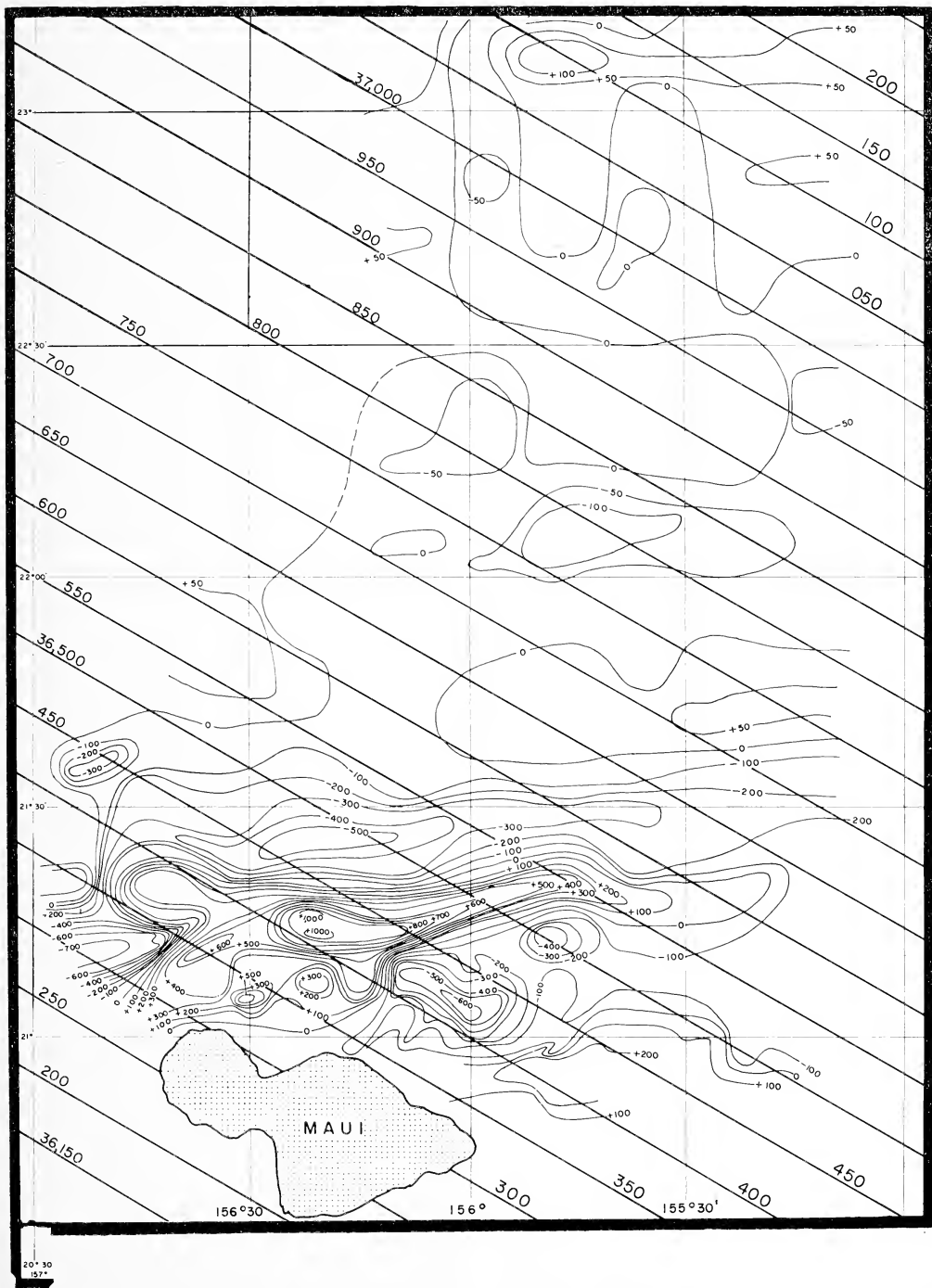


FIG. 8. Total force residual magnetic anomalies of ocean area north of Maui. Contour interval at 50 gammas. Heavy lines indicate regional total magnetic intensity.

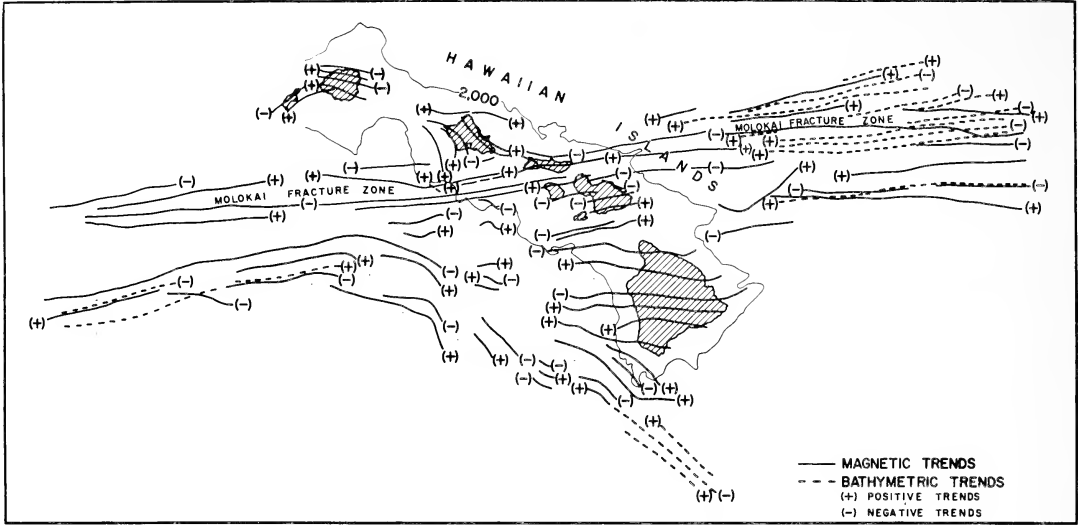
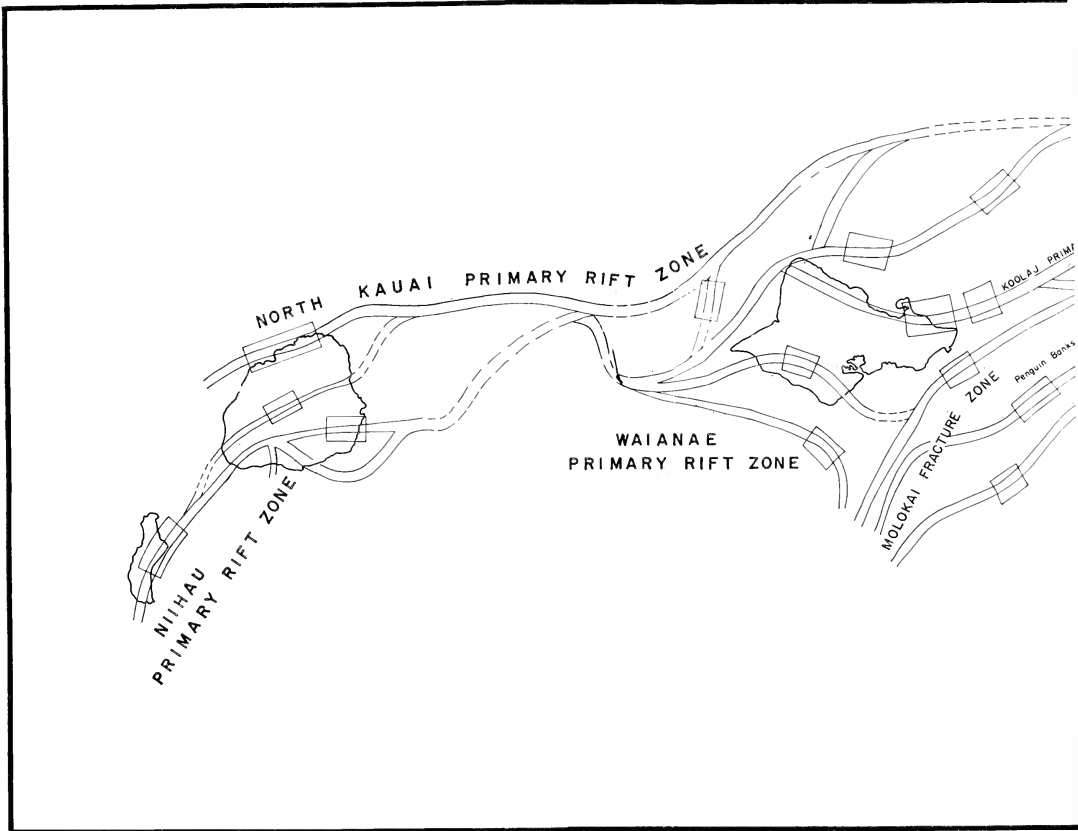


FIG. 9. Magnetic and topographic trends over the Hawaiian Rise.

FIG. 10. Sketch of primary rift zones and volcanic pipe zones, Oahu to Hawaii islands.



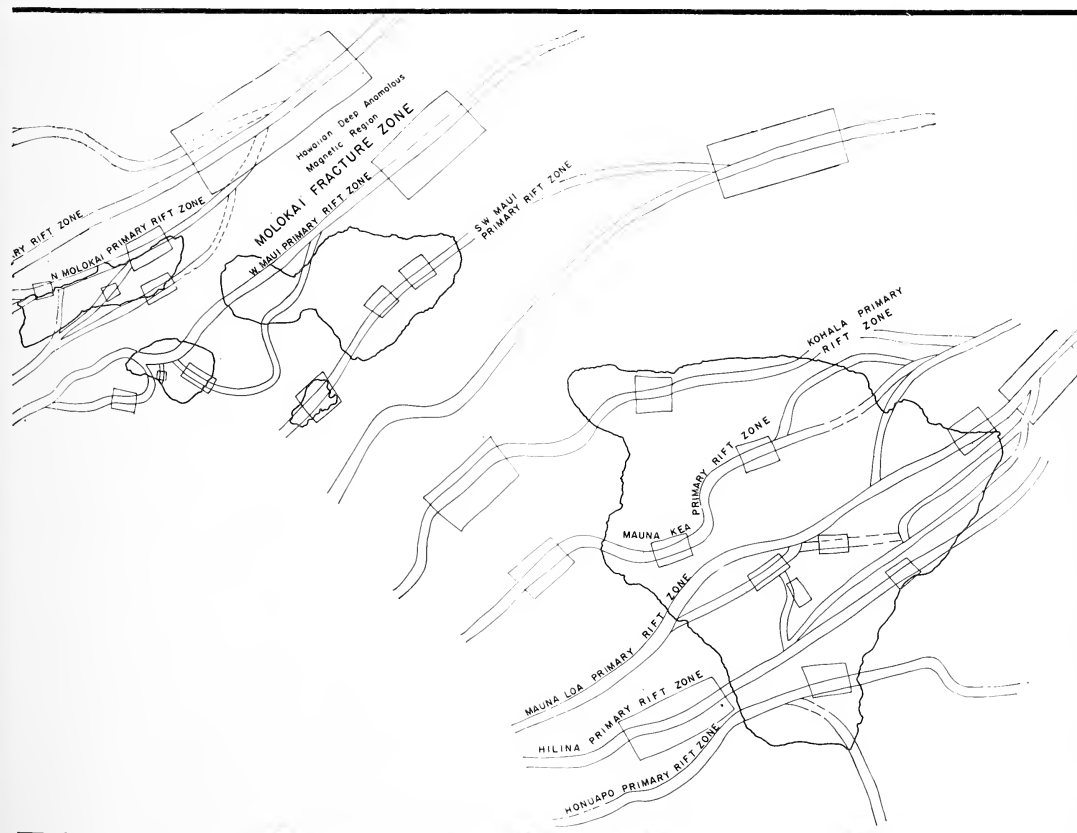
the strike of the Molokai Fracture Zone, the island of Molokai probably marks the area of intersection of two tectonic trends. Probably the older one strikes parallel to the axis of the Hawaiian Ridge, and the other strikes parallel to the Molokai Fracture Zone.

In order to assess quantitatively the nature of the magnetic anomalies and their association with geologic and tectonic features, it is best to carry out those analyses over areas of known geology. Therefore, the magnetic field has been analyzed on an individual basis for each major island of the Hawaiian Ridge.

General Remarks on Geology of the Hawaiian Islands

The Hawaiian Islands represent a series of basaltic shields that developed from the outpourings of lava from a number of primary volcanic vents. These, in turn, appear to have been located on a major crustal rift zone that is now defined by the Hawaiian Ridge extend-

ing some 2000 km from Kure Island to the island of Hawaii. Because volcanism appears to have been a progressive phenomenon, with the island of Hawaii representing the most recent addition to the Ridge, the fracture zone appears to be one that is undergoing continuous development. An alternate interpretation proposed by Wilson (1963) is that there was only one center of volcanism and that the Ridge developed by crustal migration to the northwest away from Hawaii. The continuity in strike of the Molokai and Murray fracture zones across large reaches of the Pacific Ocean and the Hawaiian Ridge, however, tends to discount this rather intriguing theory. As indicated earlier, the present magnetic study indicates that there are major anomalies associated with known fracture systems, such as the Molokai Fracture Zone, and with implied fractures in the crust and primary centers of volcanism. In each case, the intrusion of rock at depth having a high magnetic susceptibility is indicated.



Measurements of dike rocks collected in the islands have shown that, in general, the susceptibility and remanent magnetization in these intrusive rocks are higher than that in the surrounding extrusive rocks by a factor of two. These relations verify the results of theoretical analyses of the anomalies, and suggest that most of the magnetic anomalies in the Hawaiian Islands are explainable by having magnetic intrusive rocks occupy the rift zones and the primary volcanic vents responsible for the formation of the islands.

Island of Hawaii

GEOLOGY OF HAWAII: Since the geology of the island of Hawaii has been described in detail by Stearns and Macdonald (1946), it is reviewed here only briefly. The rocks constituting this island are basalts and their differentiates, whose magnetic susceptibilities vary between 2.6×10^{-3} and 0.2×10^{-3} cgs units. Because the intensity of remanent magnetization is approximately 10 times the numerical value of the susceptibility, it has not been possible, in general, to discriminate between the magnetic effects of the individual formations. As will be seen, the principal magnetic anomalies are associated primarily with intrusive features such as centers of volcanism and dikes.

Although the island is only 93 miles long and 76 miles wide, Stearns and Macdonald identify five major volcanic centers: Kohala Mountain, Mauna Kea, Hualalai, Mauna Loa, and Kilauea. The earliest eruptions appear to have taken place in Tertiary time.

Hualalai Volcano was active from Tertiary to Recent time and has erupted basalts and trachyte along three rift zones. In 1801 an eruption produced olivine basalt with a large proportion of ultrabasic to dioritic inclusions.

Kohala Mountain is built largely of olivine basalts, tholeiitic basalts, and ash erupted along three rift zones trending across the summit of the volcano. Most of the activity was during the Middle Pleistocene. Caldera faults defining a shallow graben containing alkalic basalt now mark the summit area.

Mauna Kea, the highest of the volcanoes, is composed of tholeiitic basalt with a capping of alkalic basalt and ash, erupted along three rift zones trending away from the summit. The

volcano was active from the Pleistocene to Recent, and the summit is now marked by several large cinder cones.

Mauna Loa, the largest and second highest volcano in Hawaii, is located adjacent to Mauna Kea. It is active periodically and has erupted olivine basalt along two rift zones. A large caldera marks the summit.

Kilauea is the smallest and currently the most active of the volcanoes. It is located at the intersection of two rift zones.

Although, as seen, rift zones defined by surface fissures and chains of volcanic cones which usually intersect at the summits are associated with all the volcanoes, most of these surface fissures do not have magnetic anomalies associated with them. Thus the surface fissures appear to be superficial features. Figure 11 shows their locations and identifies the individual volcanoes with which they are associated. It is along these rifts that most of the recent flank eruptions have occurred. Their locations suggest that they have originated from the dilatational forces associated with the development of the individual volcanic shields.

Similarly, there are normal faults (Fig. 12) which appear to be superficial features that have resulted from the rapid growth of the volcanic shields. These are of three types: (1) circular or concentric faults originating around pit craters (calderas), (2) faults parallel to rift zones, and (3) faults near the coast, dipping seawards. The horizontal extent of these faults, which are generally less than 10 miles in length, is small. Continuous strike directions are uncommon.

A comparison between the superficial structural patterns and deep-seated features such as the primary rifts and volcanic vents on the island of Hawaii can best be made by comparing Figures 11 and 12 with 13, which presents the total force intensity magnetic map of the island. As seen from Figure 13, the summits of all five volcanoes on the magnetic map are marked by dipole anomalies polarized normally; i.e., with the positive pole to the south and the negative pole to the north. Because at the magnetic latitude of Hawaii a dipole effect will be produced by nearly vertically sided bodies whose vertical dimensions are in excess of the minimum horizontal dimension by a factor of two or

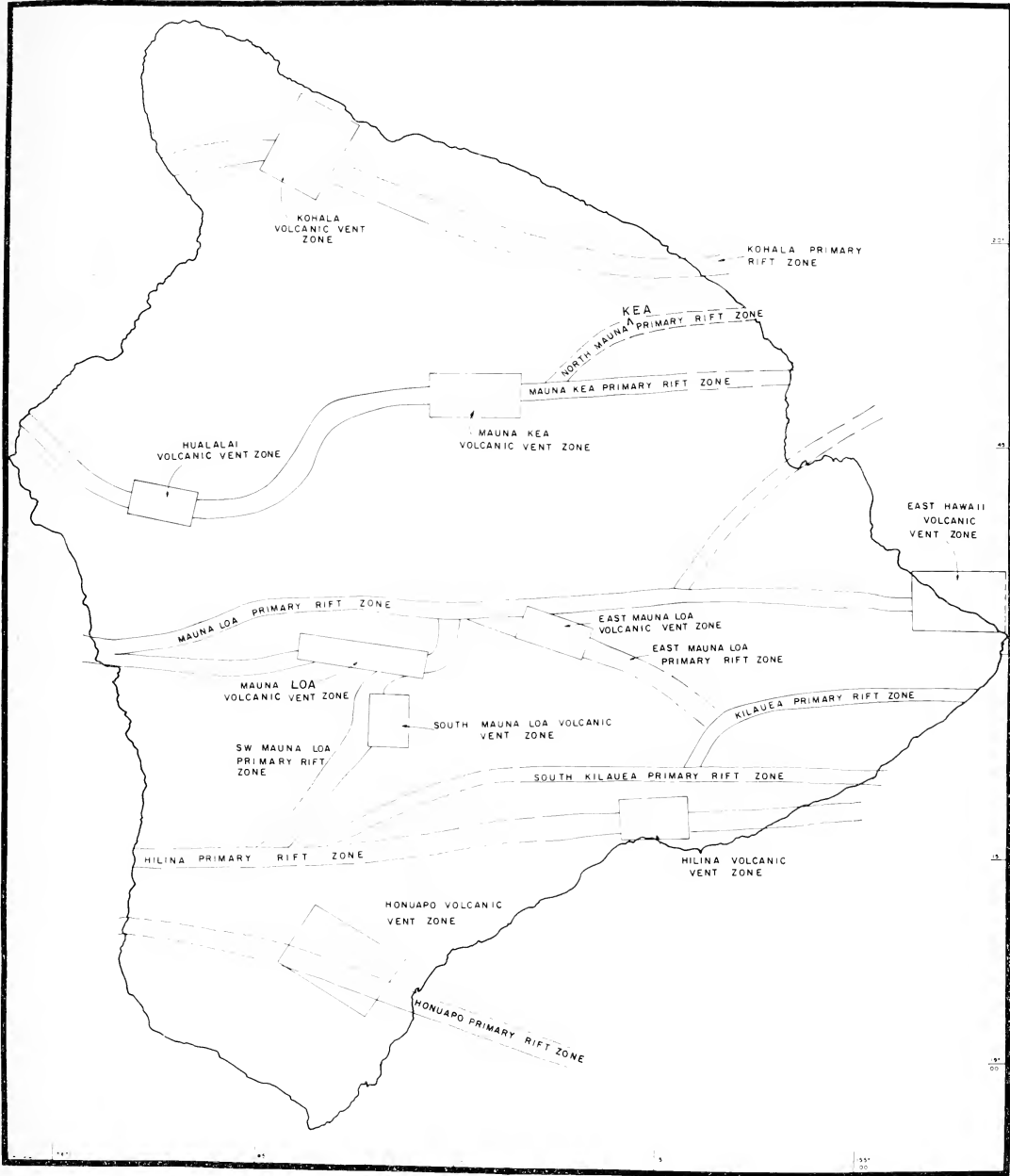


FIG. 11. Primary rift zones and volcanic pipe zones for the island of Hawaii.

greater, the points of inflection on the profiles across the dipoles mark approximately the center of the anomalous body. Lenticular magnetic gradients defining dipoles persisting for long horizontal distances, such as the one striking in an east-west direction north of Mauna Loa, are interpreted as being due to intrusive rock in

major crustal fractures. On this basis, the magnetic anomaly field of Hawaii can be subdivided as follows:

a. Dominantly east-west striking primary rift zones probably representing intrusions derived from considerable depths that are occupying primary fractures in the crust.

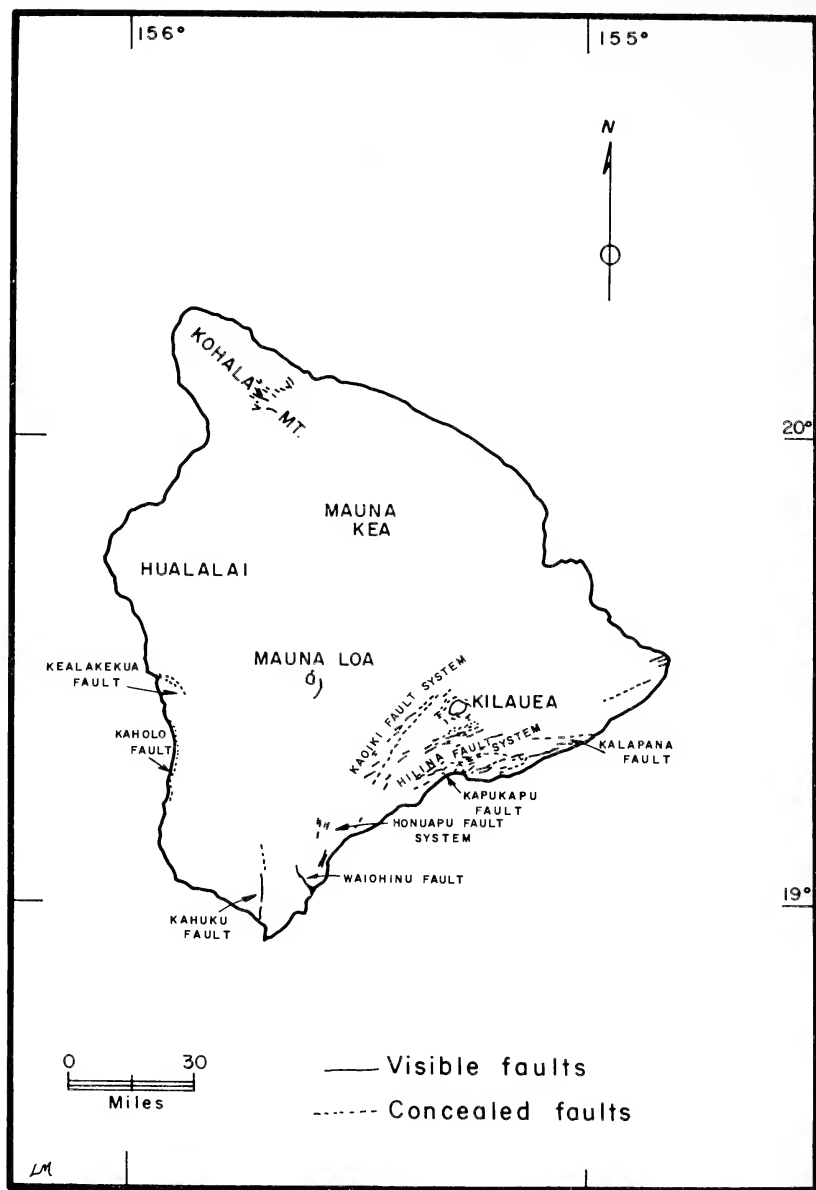


FIG. 12. Map of the island of Hawaii showing location of visible and concealed faults. (From Stearns and Macdonald, 1946.)

b. Dipole centers associated with volcanic vents. It appears significant that all these volcanic center anomalies are located on the axes of the principal longitudinal anomalies related to primary crustal rift zones, and that the latter, in general, do not coincide with secondary fracture systems.

Some superficial rift zones, such as the south-

west rift zone on Mauna Loa, do have an associated magnetic effect; however, most primary rift zone anomalies (Fig. 11), such as the east-west rift zone anomaly north of Mauna Loa and the Mauna Kea-Hualalai rift zone anomaly, do not have associated superficial features. Judging from the magnetic depth estimates and sizes of the dipole anomalies, these primary rift zone

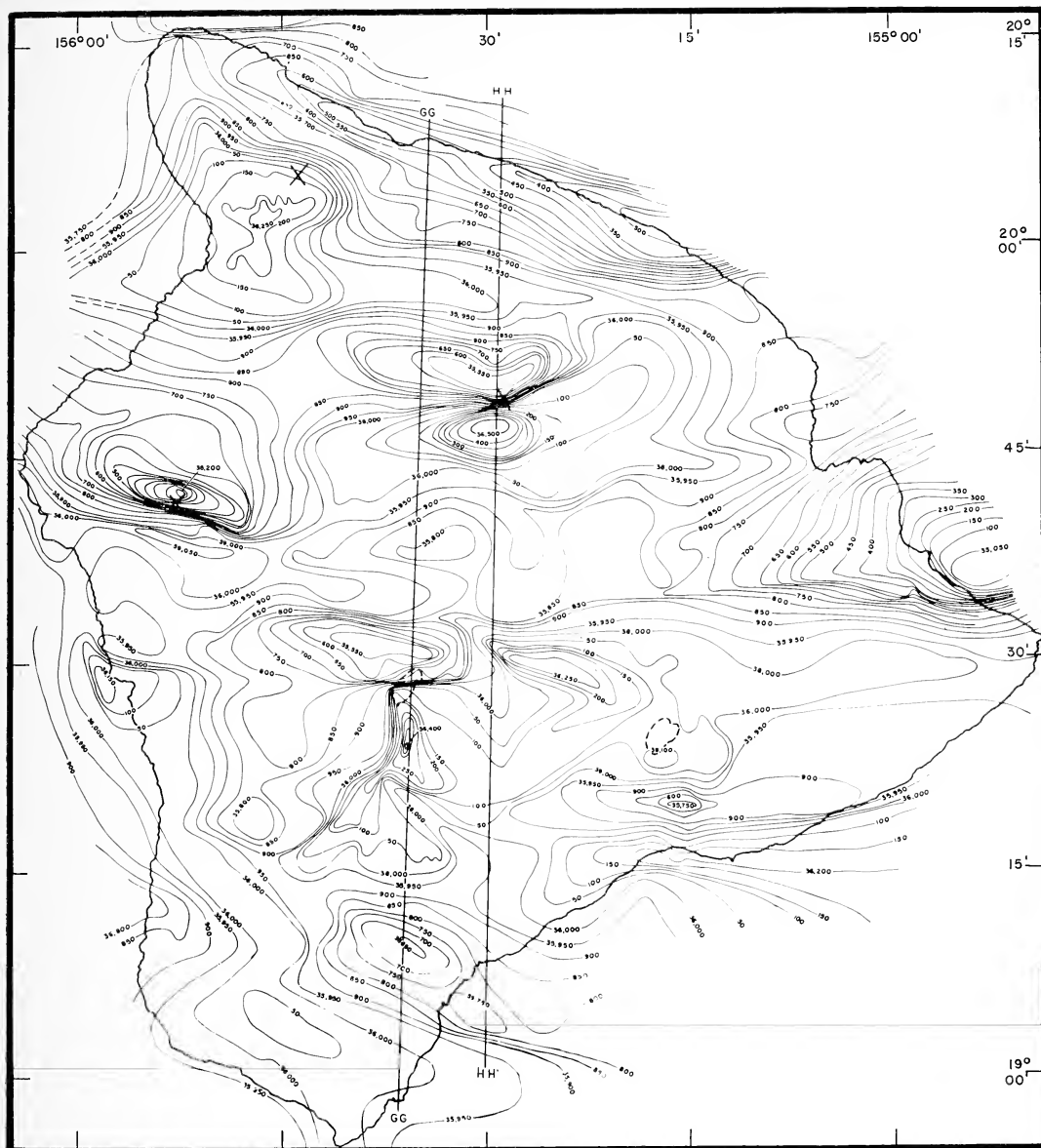


FIG. 13. Total force magnetic map of the island of Hawaii, based on aeromagnetic profiles flown at 14,000 ft over Mauna Kea and Mauna Loa, and at 12,000 ft over the rest of the island. Contour interval at 50 gammas.

anomalies originate from depths as great as 10 km below sea level. The absence of anomalies over most of the "fundamental fissures" deduced from geologic investigations can be explained only by an obvious difference in rock material from that causing the primary rift zone anomalies, and a lack of contrast in magnetic susceptibility of the intrusives filling the secondary fissures and the surrounding lavas.

Although the magnetic anomalies do not indicate that the major volcanoes are interconnected with each other except where two vents are located on the same primary rift anomaly, this possibility is not ruled out, inasmuch as a shallow connection would not have magnetic expression if the rock were above the Curie temperature.

In all cases, it is notable that the volcanic

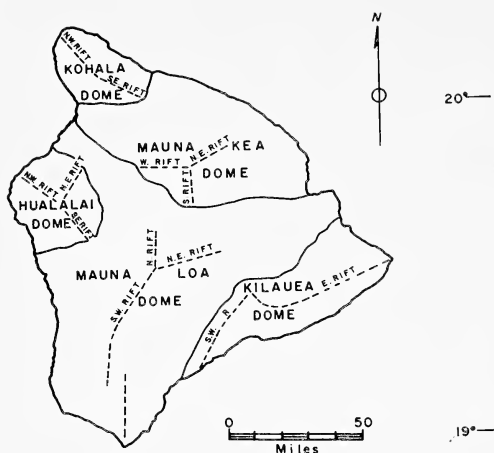


FIG. 14. Map of the island of Hawaii showing surface rift zones. (From Stearns and Macdonald, 1946.)

vents are located on the east-west primary rift anomaly zones. As discussed previously, these primary rift zones, defined by elongate dipole anomalies, are not confined to the island mass but extend into the adjacent ocean. Thus, on the island of Hawaii, moving south from Kohala Mountain, we have:

1. The "Kohala Primary Rift Zone," on which is located the volcanic center of Mt. Kohala.

2. The "Mauna Kea Primary Rift Zone," which strikes in a general east-west direction and on which are located the Mauna Kea and Hualalai vents. This primary rift zone is located some 20 miles south of the "Kohala Primary Rift Zone." The northeast rift on Mauna Kea, as shown by Stearns and Macdonald (Fig. 14), appears on the main limb of the primary rift zone, as does the west rift. However, although the south rift is reflected in the magnetic anomalies as a southward bay, it is improbable that it has any significant depth or magnetization, as the local anomaly is only $+80$ gammas. The primary rift zone apparently enters the area of Mauna Kea along the northeast rift, and changes direction beneath the west rift of Mauna Kea. The trend then experiences a southward deflection between the mountains of Mauna Kea and Hualalai and enters beneath the summit of Hualalai Volcano, continuing to strike westward out to sea. The southeast rift of Hualalai Vol-

cano is defined by a $+50$ -gamma anomaly, which disappears in the Mauna Loa Primary Rift Zone. However, the magnetic anomaly is too low, in view of the anomalies produced by the volcanic pipe complexes, to warrant an assumption that the Mauna Loa and Mauna Kea primary rift zones are interconnected at shallow depth along this rift. The northeast rift appears as a short low positive local magnetic anomaly of $+50$ gammas, which persists for only 12 km northeast of the summit of Hualalai Volcano. The northwest rift is difficult to interpret in terms of local residual magnetic anomalies, because it lies directly along the negative limb of the Hualalai magnetic anomaly.

3. The "Mauna Loa Primary Rift Zone" strikes from Cape Kumukahi westward and is marked by a magnetic low of -950 gammas located 2 miles north of the trend. The magnetic low may be interpreted as being caused by a flat shallow source of molten nonmagnetic magma (located at a depth of 5–10 km from the surface) with dimensions of 8 km by 2 km. However, because the contours of this anomaly do not close seaward, no definite statements on size or shape of the cause of this anomaly can be made. Some curious branches of this rift zone bifurcate so that the volcanic pipe complex of Mauna Loa Volcano is located on a southwestern extension of the rift zone. A secondary pipe complex of Mauna Loa is located 10 km south of Mauna Loa's summit, and probably accounts for the southern extension of the $+330$ milligal Bouguer gravity anomaly on the gravity anomaly map of the island of Hawaii (Kinoshita et al., 1963). Similarly, another pipe complex is located 15 km northeast of the summit of Mauna Loa, on a branch of the Mauna Loa Primary Rift Zone.

4. The "Kilauea Primary Rift Zone" appears as an east-west striking feature 8 km south of Cape Kumukahi, curves southward and joins an indistinct east-west striking rift zone 10 km south of Kilauea caldera. It is difficult to locate the Kilauea caldera on any of the primary rift zones. Judging from the strike of these rift zones, it appears that Kilauea Volcano originated in the zone of coalition between the southeast branch of the Mauna Loa Rift Zone and the two Kilauea rift zones. Although Kilauea caldera has a distinct gravity anomaly associated with

it, the magnetic anomaly is almost nonexistent. We can deduce from this association that the vent material beneath the caldera is dense and nonmagnetic or partially magnetic, as would be the case with a partially molten vent complex.

5. The "Hilina Primary Rift Zone" has been named after the Hilina Fault System, with which it apparently has a direct association. It is surprising that such a prominent surface feature as the Kilauea Southwest Rift has no magnetic anomalies associated with it. In fact, it cuts right across the zone of strong east-west striking anomalies. It can only be concluded from this evidence that the Kilauea Southwest Rift is only a superficial feature. The Hilina trend has a distinct, normally-polarized magnetic anomaly of 450 gammas peak-to-peak associated with it. This anomaly could be the result of intrusion along the Hilina Fault System, or it could be due to an ancient volcanic complex now submerged beneath the covering lavas of the Kilauea series.

6. The "Honuapo Primary Rift Zone" crosses the shoreline of the island of Hawaii in the neighborhood of the town of Honuapo. As seen in Figure 11, this rift zone has a vent tube magnetic dipole anomaly associated with it. No doubt this broad dipole marks the center of an extinct volcanic vent now buried.

It is important to note that the primary rift zones described above are not linear and, in places, are sharply bent, suggesting that there has been intrusion along intersecting fractures. In all cases, the rift zones probably exist, but they have not been marked on Figure 11. However, the general strike of the primary rift zones is east-west and the bending is probably the result of local differential tectonic movement on cross faults. As it is unlikely that two cross-cutting sets of fractures would be open at the same time, intrusions were not necessarily contemporaneous, but could have taken place in two stages, with the short flexure offsets in the dominant east-west trends representing leakage of magma into the joining fractures as they open up with a change in regional stress pattern. Although the point cannot be proved, it is not unlikely that vents on the primary rift zones developed at points of weakness where two sets of crustal fractures intersect.

Under this concept, the volcanoes which formed the island are secondary features superimposed on primary crustal rifts. In this respect, the writers are in agreement with the theory of Betz and Hess (1942), which proposes a fissure eruption origin for the Hawaiian Islands. However, as is evident, there is no single fault zone forming fissures from which magma erupted in mass.

Inasmuch as on Oahu the primary rift zones are oriented northwest-southeast and strike parallel to the axis of the Hawaiian Ridge rather than east-west, as they do on Hawaii, Maui, and Molokai; and inasmuch as both trends are present on Kauai, it appears that not only are there two sets of primary fractures associated with the Hawaiian Islands, but also that intrusion into them must have been governed by a change in regional stress pattern whereby the northwest-southeast sets were closed after the development of Oahu. Although the primary rifts are oriented east-west, it is the continuation of the Ridge along this same general strike that constitutes the principal argument for the centers of volcanism in Hawaii being localized at points of weakness where the earlier, now-closed, northwest-southeast fractures intersect the east-west fractures that stand out so prominently in the magnetic anomaly pattern.

The lack of negative anomalies and the absence of subdued positive anomalies above the summit of Mauna Loa, which is periodically active, appear to substantiate the existence of a secondary shallow magma chamber as postulated by Eaton (1962). Similarly, the lack of any pronounced magnetic anomalies beneath the Kilauea caldera suggests the existence of such a chamber. In this respect, these two volcanoes appear to differ from the other Hawaiian volcanoes, all of which have marked dipole anomalies associated with the vents.

QUANTITATIVE INTERPRETATION OF THE MAGNETIC ANOMALIES OVER THE ISLAND OF HAWAII: Depth, size, and shape estimates of the volcanic pipe zones, together with comparable model studies, are presented in Table 2.

As indicated earlier, rocks from 30 exposures were sampled on the island of Hawaii and analyzed in the laboratory for susceptibility,

using a susceptibility bridge, and for comparative remanence, using an astatic magnetometer. The samples ranged from tholeiite, collected from the Kilauea caldera walls, to alkalic basalt, collected from the area of recent eruption in the Puna district and from the 1919 and 1929 Mauna Loa lava flows. Olivine nodule-rich lava samples were also collected from the 1801 Hualalai lava flow. The susceptibilities ranged from 1.54×10^{-3} cgs units for tholeiite to 3.62×10^{-3} cgs units for samples of recent alkaline basalt. However, it should be noted that the susceptibilities of even neighboring samples of the same lava flow may vary by as much as $\pm 1.0 \times 10^{-3}$ cgs units, depending on the absence or presence of local concentration of ferromagnetic minerals. Samples from rock quarries of massive fine-grained basalt, such as those collected in the vicinity of Kona airport, had variations of only ± 0.2 cgs units. Olivine-rich samples of alkalic basalt from Hualalai Volcano yielded susceptibilities as low as 0.37×10^{-3} cgs units. This selection of surface samples, which certainly cannot be regarded as representative of the bulk of the lavas of the Hawaiian volcanoes, does give a reasonable assemblage of representative susceptibilities.

Decker (1963) obtained an excellent fit of measured and observed profiles across the walls and floor of the Kilauea caldera, using an average value of 1×10^{-3} cgs units for susceptibility of basalt and a natural remanent magnetization of 10×10^{-3} cgs units. In the present study, the measured susceptibilities do

not deviate by more than a factor of two from the averaged values of Decker. The observed remanence values are approximately the same. The value of susceptibility of 1.5×10^{-3} cgs units and a remanence of 11.0×10^{-3} cgs units have been assumed in all the magnetic reductions and computations for the volcanoes of the Hawaiian Islands.

By using depth estimation methods coupled with theoretical model studies, depth estimates and shape and size estimates were carried out for major magnetic anomalies. In order to simplify the mathematical computations, rectangular shapes for the horizontal cross section of vents were adopted.

A summary of all the analyses is shown in Table 2. The tops of the volcanic vent zones appear to lie within a zone extending from sea level to 4 km. The top surface of the postulated Ninole vent (Stearns and Macdonald, 1942), now buried beneath flows from Mauna Loa, appears to be located at a depth of 3.4 km below sea level.

Another anomaly that is not represented by a surface feature is the Hilina volcanic vent. This feature is not reflected in the gravity anomalies (Fig. 15), yet it marks the center of a 400-gamma peak-to-peak magnetic anomaly. In the geologic cross section by Stearns and Macdonald (Figs. 16 and 17), an upwarp of the Hilina volcanic series, as well as a system of faults, is shown to occur in the vicinity of the point of inflexion of the magnetic anomaly. Therefore, the Hilina magnetic anomaly (Figs.

TABLE 2
ANALYSES OF THE TOTAL FORCE MAGNETIC ANOMALIES OVER THE ISLANDS OF HAWAII

1*	2*	3*	4*	5*	6*	7*	8*
Kahuku pipe complex	3.05	14.5 by 09.5	6.5	-3.40	2.30×10^{-3}	400	5
Mauna Loa pipe complex	4.30	16.8 by 04.0	2.7	+1.60	6.95×10^{-3}	800	20
Hualalai pipe complex	3.05	8.8 by 04.9	1.3	+1.75	6.95×10^{-3}	800	15
Kohala pipe complex	3.05	8.8 by 11.2	5.7	-2.65	14.00×10^{-3}	800	10
Hilina pipe complex	3.05	9.6 by 05.6	4.0	-0.95	11.30×10^{-3}	400	12
Mauna Kea pipe complex	4.30	12.0 by 06.0	1.9	+2.70	13.80×10^{-3}	1500	8

1* Name of feature.

2* Elevation of flight level above sea level in kilometers.

3* Cross sectional size of anomalous body in kilometers from the total magnetic intensity map.

4* Depth estimates to top of anomalous body in kilometers (Vacquier method).

5* Top of anomalous body with respect to sea level in kilometers.

6* Magnetization contrast of anomalous body with surrounding rock in cgs units (Vacquier method).

7* Maximum amplitude of anomaly in gammas peak-to-peak.

8* Length of anomalous body in kilometers from theoretical models.

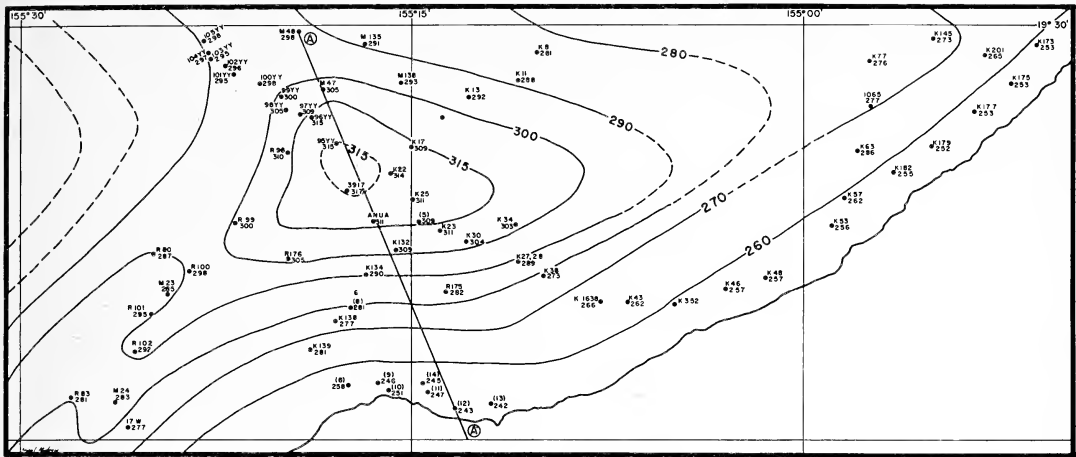


FIG. 15. Bouguer anomaly map of the Kilauea area on the island of Hawaii, $\rho = 2.3$ gm/cc. Contour interval at 10 mgals. (After Kinoshita et al., 1963.)

17 and 18) probably marks an inactive center of volcanism containing more magnetic rocks than the surrounding basalts but having the same density as the surrounding basalts. The top of this center appears to be buried now at a depth of 0.95 km below sea level beneath the lava flows of Kilauea.

Also, the top of the Kohala volcanic vent appears to be located at a depth of 2.65 km beneath sea level.

The remaining major magnetic anomalies representing the vents for Mauna Loa, Mauna Kea, and Hualalai volcanoes occur at depths located above sea level. The Mauna Loa vent appears to originate from a depth of 1.9 km above sea level, and the Mauna Kea vent appears to originate from a depth of 2.7 km above sea level. The Hualalai vent has a depth of 1.75 km above sea level. It is difficult to judge the overall accuracy of the depth estimation

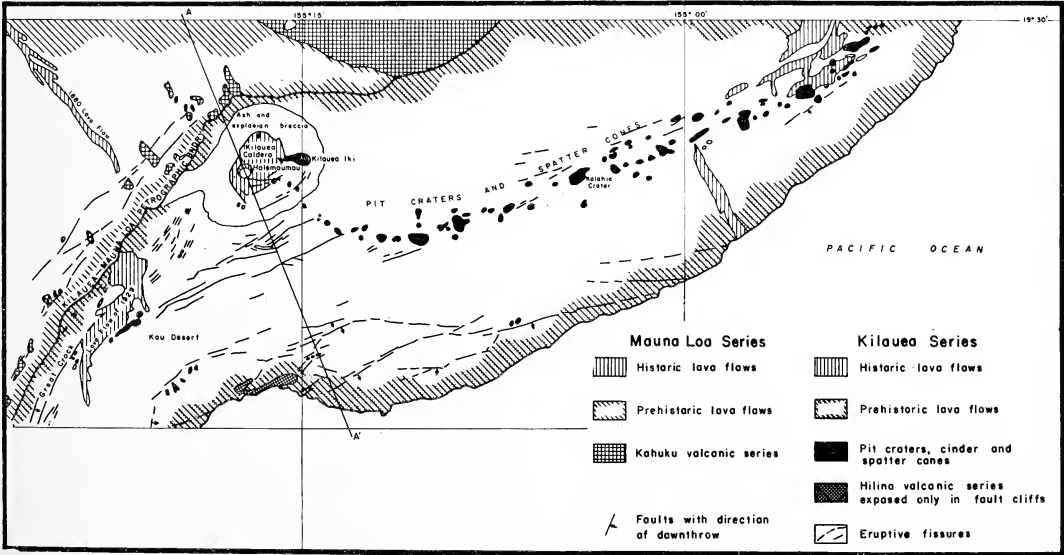


FIG. 16. Map of the geology of Kilauea Volcano, island of Hawaii.

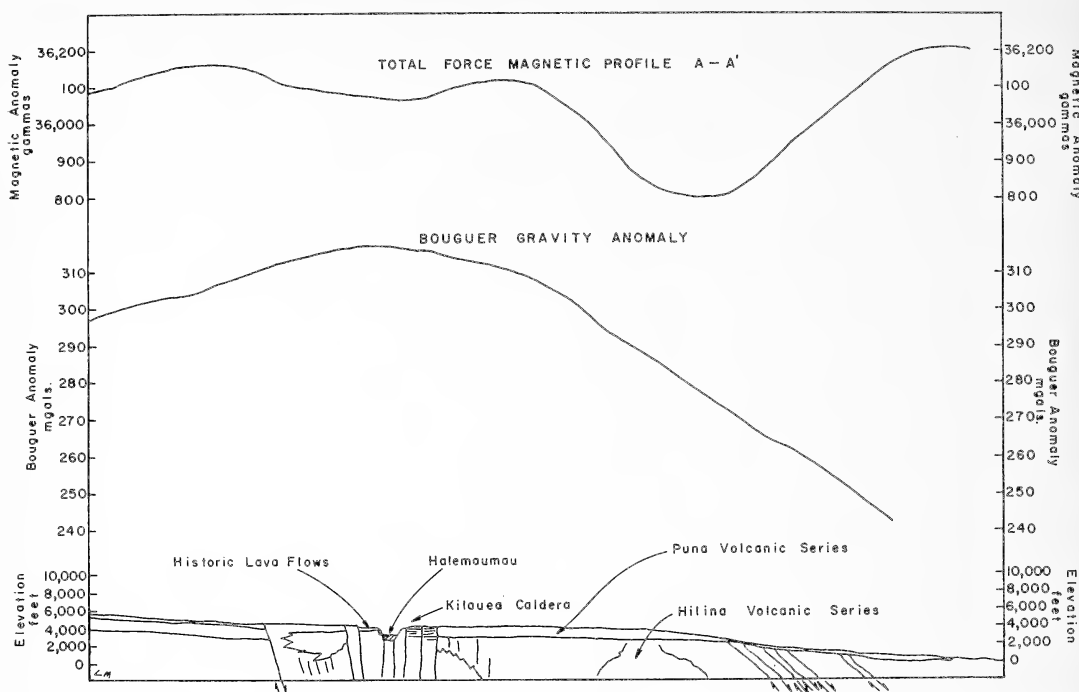


FIG. 17. Implied geological cross-section across Kilauea Volcano, island of Hawaii, with magnetic and gravity profiles along line A-A' (see Figs. 16 and 18).

methods. However, the writers believe that, because the total force magnetic dipole anomalies are distinct and can be reasonably approximated by Vacquier models, the G indices for the magnetic anomalies of Hawaii cannot be in error by more than 0.5 km.

The apparent susceptibility contrast between the rocks of the volcanic vent complexes, calculated by using Vacquier's relationships, varies between 2.3×10^{-3} cgs units for the Ninole vent and 14.0×10^{-3} cgs units for the Kohala vent.

It is obvious from a study of Figure 16 and the above data that the horizontal dimensions of all the vent complexes are in excess of their geologic expression. This difference might well reflect the presence of shallow magma chambers as postulated by Eaton (1962), or represent a spreading of the vent zone at depth, as suggested by analyses of the gravity anomalies associated with vents. Judging from the analyses of the vertical dimensions of the volcanic vent zones, the intrusive rock complex in the vents on the island of Hawaii extend upward from a

depth of 19 km below present sea level (some 4–5 km beneath the present level of the Mohorovicic discontinuity) to near the present surface. It is important to note though, that the bottom level of a 20-km-long vent zone may be varied by as much as 3 km without influencing the total anomaly profile by more than 5–20 gammas. Similarly, the bottom of the vent zone may be raised or lowered by several kilometers by altering slightly the general susceptibility contrast or natural remanent magnetization.

Inasmuch as the top of the Ninole vent complex lies at the deepest level, it could represent the oldest vent, but this is by no means certain. Certainly one would not interpret the fact that the top of the vent complex associated with Mauna Kea Volcano stands higher than that associated with Mauna Loa as indicating that it is the younger of the two.

MAGNETIC EFFECT OF TERRAIN ON THE ISLAND OF HAWAII: As stated previously, the flight elevations for taking the profiles in Hawaii were chosen so as to minimize the effect of terrain. All of the magnetic profiles used in

the magnetic computations were corrected for terrain at the flight level at which the magnetic readings were recorded.

The largest topographic effect was produced by the peak of Mauna Kea, where the aeromagnetic profiles, out of necessity with the light plane used, were taken at an elevation of only 300 ft above the highest point. The maximum effect of terrain above this point was +600 gammas (Fig. 19). As seen from Figure 19, the terrain correction here changed the magnetic profile to a textbook-type symmetrical dipole profile. The magnetic effect of the flank of Mauna Loa on the same profile was +190 gammas. The reason for this relatively low terrain effect on Mauna Loa lies in the greater height of the level of observation above ground surface. The terrain effect of Kohala Mountain was +100 gammas, and that of Hualalai Mountain, on the same profile, was +130 gammas. As indicated, a magnetic susceptibility of 10.0×10^{-3} was used in computing all of the effects of terrain. It should be noted that, because the topographic slope of the terrain was considerably less than 35° , the inclination of the earth's magnetic field in Hawaii, the topographic terrain correction in every case produced only a positive effect.

Because the magnetic terrain corrections did not alter the shape of the magnetic anomalies to any great extent even over Mauna Kea, it was not essential to correct the total magnetic force

anomaly map of Hawaii (Fig. 13) for topographic effects on the magnetic field.

Islands of Maui and Kahoolawe

GEOLOGY OF MAUI: Maui is the second largest island in the Hawaiian group and was formed by two volcanoes. East Maui contains the 10,025-ft high Haleakala Volcano and West Maui contains a deeply dissected volcano 5,788 ft high.

The flat isthmus connecting the two volcanoes was made by lavas from East Maui banking against the flows from West Maui. The oldest rocks on East Maui are the Honomanu basalts, which were extruded in the Pliocene or early Pleistocene period along three rift zones (Stearns and Macdonald, 1942) to form a shield about 8,000 ft high. Covering this dome are the Kula volcanics extruded in early or middle Pleistocene time. These consist of hawaiites, ankaramites, and related alkalic basalts. Volcanic activity was renewed in the middle to late Pleistocene and continued at least until about 1750 A.D., when the Hana lavas were deposited. During early Pleistocene time, it is probable that Maui, Kahoolawe, Lanai, and Molokai were joined as one island.

West Maui is composed of the older tholeiitic Wailuku basalts extruded in the Pliocene or early Pleistocene along two rifts and a set of radial fissures. The basalts form a shield 5,600 ft high. Iao Valley marks the center of the

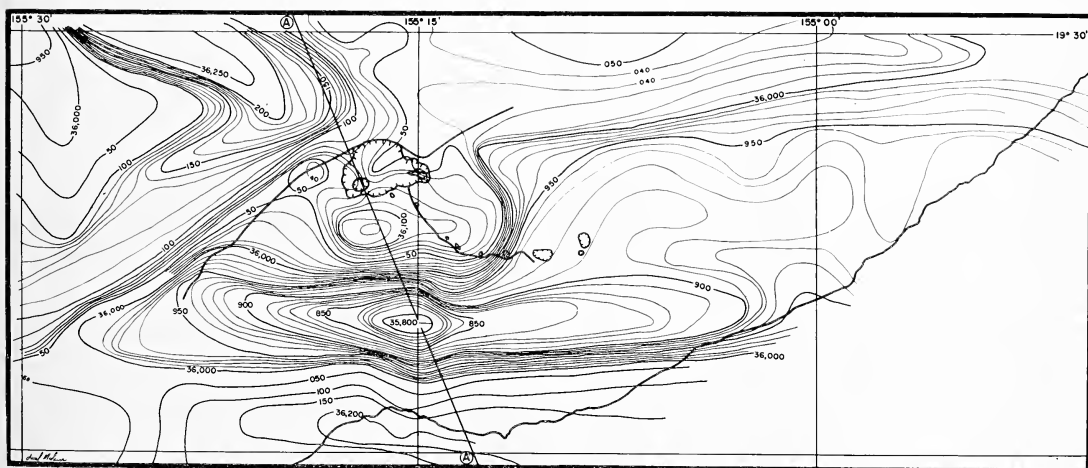


FIG. 18. Magnetic anomalies of Kilauea Volcano, island of Hawaii, flown at an elevation of 10,000 ft. Contour interval at 10 gammas.

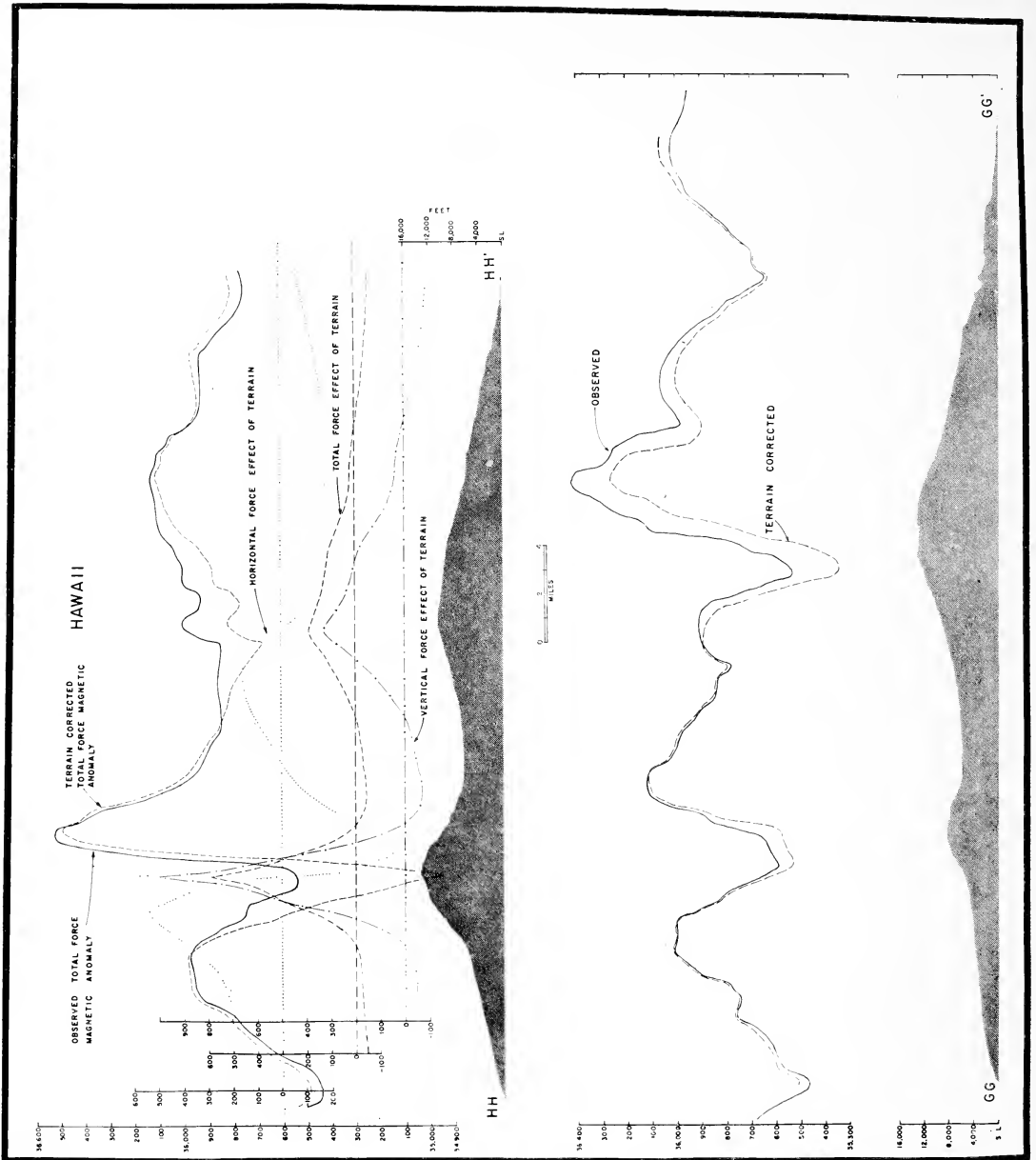


FIG. 19. Terrain-corrected magnetic profiles (above) HH-HH' and (below) GG-GG' along the island of Hawaii (see Fig. 13).

eroded caldera of this shield. Over this shield there is a thin veneer of Honolua soda trachytes and mugearites. These were extruded in the late Pliocene (?) or early Pleistocene time.

Generally, the flows on Maui, according to Stearns and Macdonald (1942), were fed by magma that rose through fairly straight, vertical,

narrow fractures (Fig. 20). At depth, the dikes are massive and cross-jointed; and, where they underlie rift zones, they form dike swarms 1-3 miles wide. Bosses and plugs on West Maui range from 100 to 3,000 ft in diameter.

GEOLOGY AND GEOLOGIC STRUCTURE OF KAHOO LAWE: Because it appears from the mag-

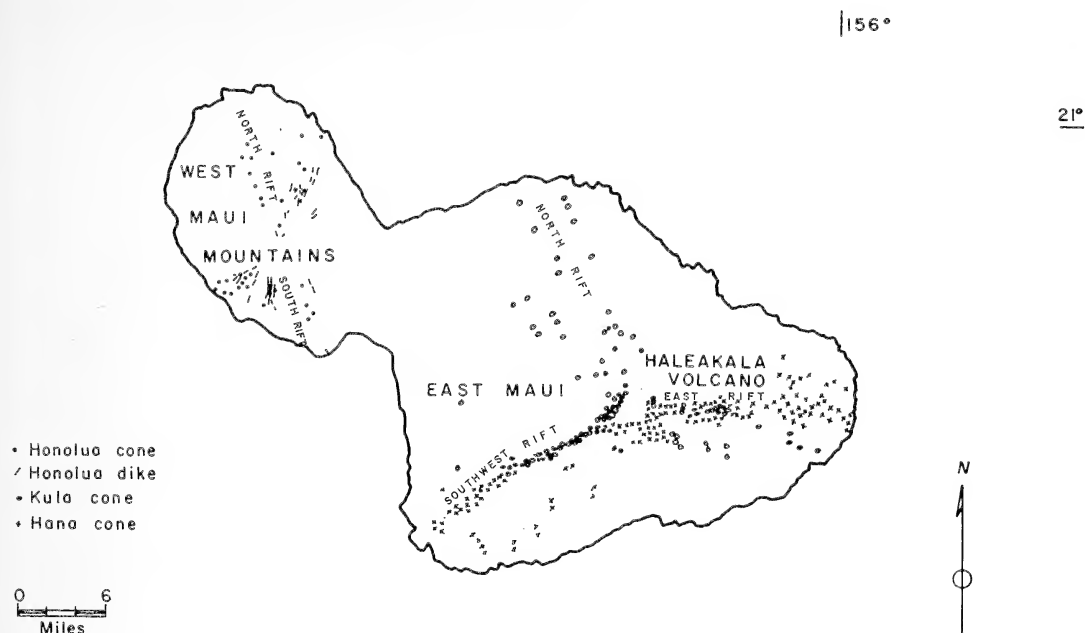


FIG. 20. Vents of the Hana, Kula, and Honolua volcanic series, and associated rift zones, island of Maui. (From Stearns and Macdonald, 1946.)

netic surveys that the island of Kahoolawe lies on the Southwest Primary Rift Zone defined on Maui, the magnetic field relations to geology on Kahoolawe are considered along with those for Maui.

Kahoolawe Island, according to Stearns (1940), is a shield-shaped, extinct volcano, 11 miles long, 6 miles wide, and 1,491 ft high, lying $6\frac{3}{4}$ miles southwest of Maui. The island consists chiefly of tholeiite erupted from three rift zones and a vent at their intersection. The strike and position of these rift zones is defined by dike patterns in cliff faces and from the alignment of cinder cones present.

THE MAGNETIC FIELD OVER THE ISLANDS OF MAUI AND KAHOOLAWA: From an inspection of the total force magnetic map (Fig. 2), it appears that Maui was formed from eruptions on two east-west trending primary rift zones similar to those described on the island of Hawaii. Geologic observations in Haleakala Crater show that the southwest primary anomaly trend on Maui parallels the geologic East Rift and Southwest Rift of Stearns and Macdonald (1942). The surface manifestations of the Southwest Maui Primary Rift Zone anomaly, therefore, appear to be these two rift zones. The analysis

of this primary rift zone defines a belt of magnetic rocks two miles wide. As elsewhere, the natural remanent magnetization of dike rocks collected in Haleakala Crater by Malahoff was approximately 10 times the intensity of the surrounding lavas, although the petrographic composition of both the lavas and dike rocks was essentially the same. The direction of polarization of these dike rocks from Haleakala was normal.

Figure 21 shows that there are two principal centers of volcanism on the southwest primary rift zone anomaly, one marked as East Haleakala Volcanic Vent and the other as West Haleakala Volcanic Vent. Another volcanic vent zone is indicated on the same rift zone and has been named Kahoolawe Volcanic Vent, which is defined by a normally polarized dipole over the island of Kahoolawe (Figs. 22 and 23).

Although the West Maui Primary Rift Zone anomaly strikes in the same general direction as does the southwest primary rift zone anomaly, there is no connection between the two magnetic anomalies. It appears, therefore, that the two volcanic shields of East and West Maui originated along two separate primary rift zones. The isthmus between the two portions of Maui,

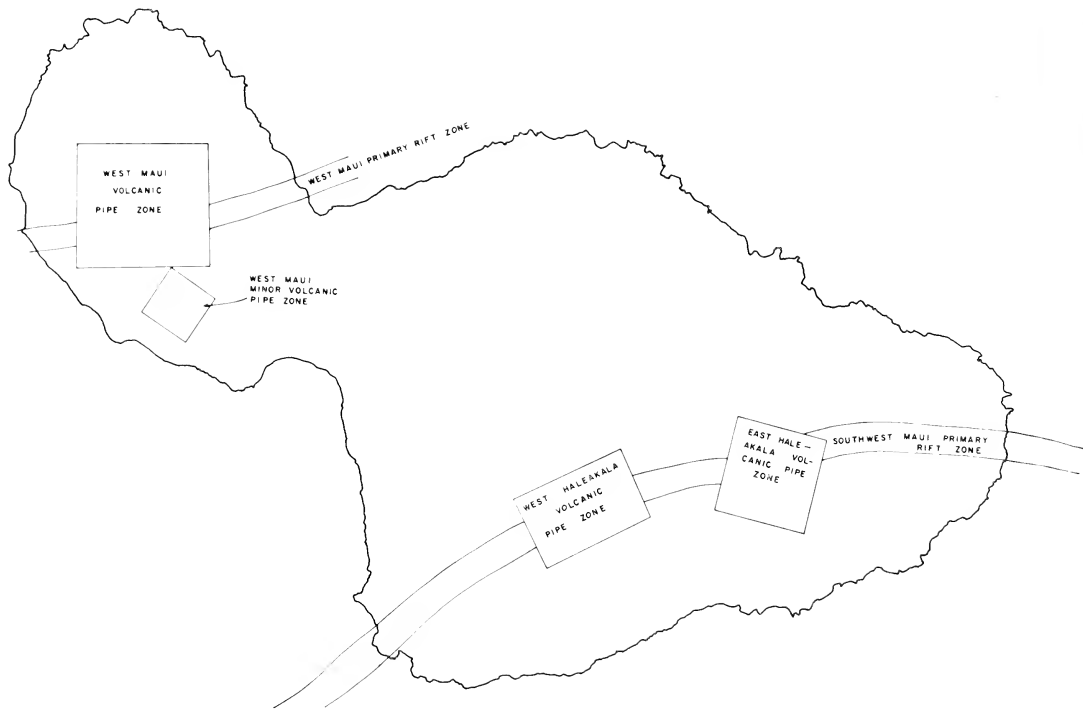


FIG. 21. Sketch of the primary rift zones and volcanic pipe zones of the island of Maui.

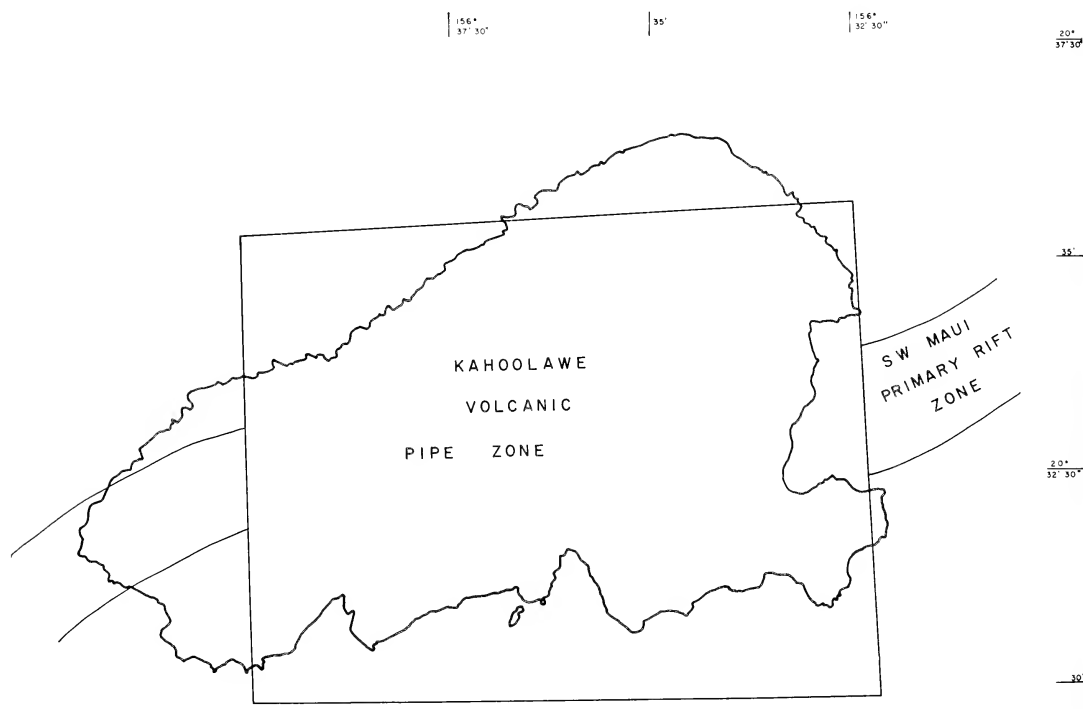


FIG. 22. Sketch of the primary rift zones and volcanic pipe zone of the island of Kahoolawe.

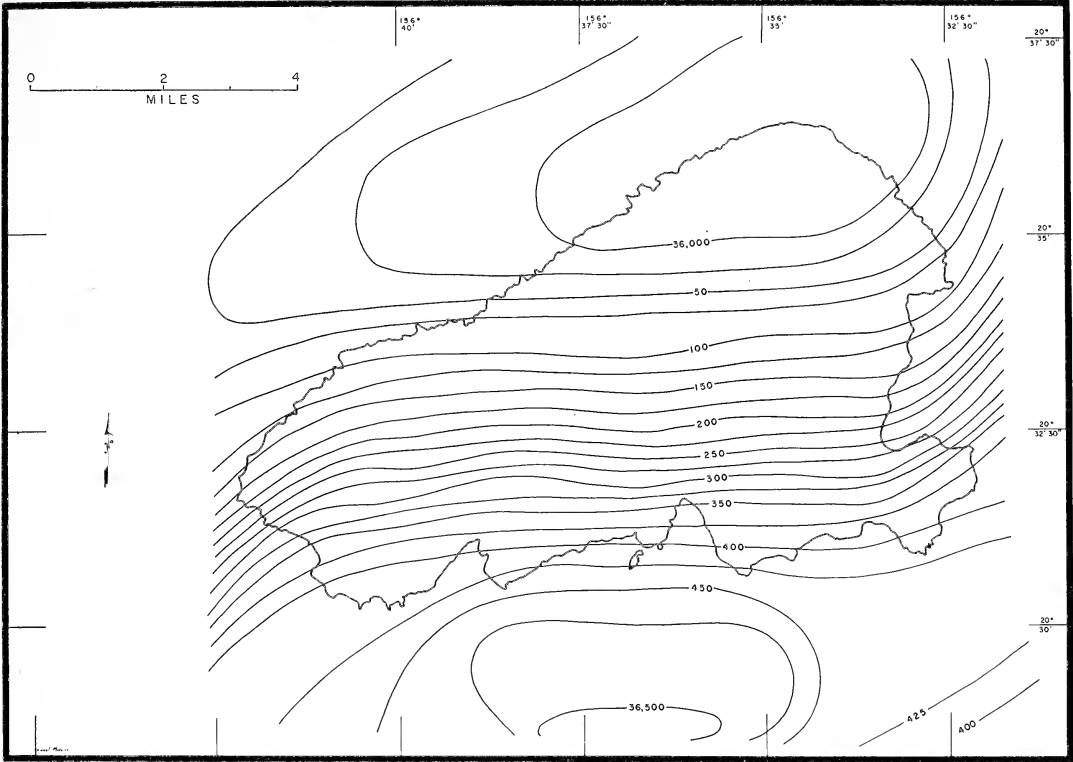


FIG. 23. Total force magnetic map of the island of Kahoolawe, based on aeromagnetic profiles flown at 8,000 ft. Contour interval at 25 gammas.

TABLE 3
ANALYSES OF MAGNETIC ANOMALIES OVER THE ISLAND OF MAUI

1*	2*	3*	4*	5*
East Haleakala Volcanic Pipe Zone	4.0	7.3 by 07.3	15 approx.	16.0×10^{-3}
West Haleakala Volcanic Pipe Zone	3.3	8.0 by 06.4	12	18.0×10^{-3}
West Maui Volcanic Pipe Zone	1.6	9.5 by 08.9	9	5.0×10^{-3}
West Maui Minor Volcanic Pipe Zone	0.5	4.0 by 04.0	3	3.0×10^{-3}
Kahoolawe Volcanic Pipe Zone	2.4	10.0 by 12.8	2	7.0×10^{-3}

1* Name of feature.
2* Depth to top of anomalous body below ground level in kilometers.
3* Approximate horizontal cross section of anomalous body in kilometers.
4* Vertical length of anomalous body in kilometers.
5* Magnetization contrasts between anomalous body and surrounding rock in cgs units.

as well as the shelf area between the isthmus and the island of Kahoolawe, is devoid of any anomalies, suggesting that this area is clear of any intrusives. A negative embayment of 30–70 gammas in the contours north of the West Haleakala Volcanic Vent anomaly suggests that a shallow north-striking zone of dikes is present within the lavas of the Haleakala dome. At its southern end, the zone of dikes, as suggested by the magnetic anomalies, is offset westward by a distance of six miles from the geologically defined North Rift Zone of Stearns and Macdonald (Fig. 20). This offset is so great that it is highly unlikely that the two are related.

QUANTITATIVE ANALYSIS OF THE MAUI AND KAHOOLOWE MAGNETIC ANOMALIES: As on Hawaii, selected magnetic profiles were corrected for the magnetic effects of topography before quantitative analysis was attempted. Using analysis techniques, as described earlier, depth and size estimates, and magnetization contrasts were derived for the anomalies of Maui. These values are listed in Table 3.

All the magnetic anomalies, with the notable exception of the West Haleakala Volcanic Vent anomaly, are reflected also by gravity highs (Kinoshita and Okamura, 1965) which suggest that, as on the island of Hawaii, the magnetic anomalies are due to dense, highly magnetic, intrusive rocks located within the volcanic vents. The West Haleakala Volcanic Vent, as defined by a single dipole anomaly, appears to

be of shallow origin and only 2 km thick, though broad in horizontal cross section.

As on the island of Hawaii, the anomalous geologic bodies giving rise to the magnetic anomalies all appear to be vertically oriented.

The apparent reversals in the direction of magnetization observed for the two West Maui magnetic anomalies could be due to reversely polarized rocks occupying the vents or to weakly magnetized rocks occupying the vents. It may be significant that weakly magnetized rocks were collected from intrusive rocks of the Wailuku series. The surrounding basalts of the same series recorded higher remanence effects of 9×10^{-3} cgs units.

Island of Molokai

GEOLOGY: The geology of this island has been described by Stearns and Macdonald (1947). The island was formed by eruptions from two principal volcanoes, West Molokai and East Molokai. West Molokai now stands 1,300 ft and East Molokai 4,900 ft above sea level. Both volcanoes were built up from the sea floor, probably during Tertiary time.

East Molokai is built of basaltic lavas with a thin cap of mugearites. Dikes cut the lower members of the volcano and trend east and northwest. On the basis of the dips of the flows the main volcanic center lies north of the present coastline. Intrusive rocks are common, and consist of stocks, plugs, and dikes which occur

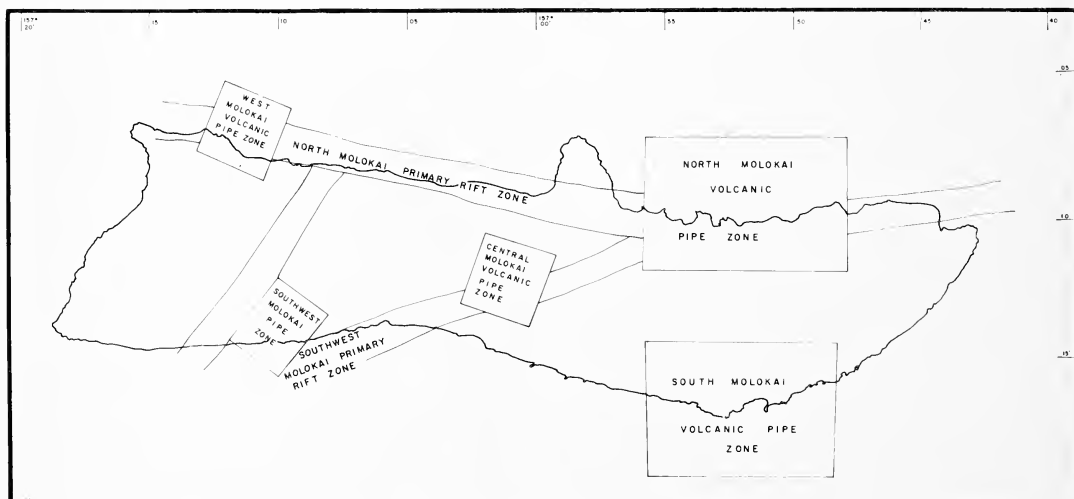


FIG. 24. Sketch of the primary rift zones and volcanic pipe zones of the island of Molokai.

TABLE 4
ANALYSES OF TOTAL FORCE MAGNETIC ANOMALIES OVER THE ISLAND OF MOLOKAI

1*	2*	3*	4*	5*
North Molokai Volcanic Pipe Zone	0.8	14.0 by 10.0	8	12.4×10^{-3}
South Molokai Volcanic Pipe Zone	1.0	13.0 by 09.5	10	6.9×10^{-3}
Southwest Molokai Volcanic Pipe Zone	0.2	4.8 by 05.6	10	7.7×10^{-3} (reversed)
West Molokai Volcanic Pipe Zone	0.3	4.8 by 05.2	10	13.9×10^{-3}

1* Name of feature.
2* Depth to top of anomalous body below ground level in kilometers.
3* Approximate horizontal cross section of anomalous body in kilometers.
4* Vertical length of anomalous body in kilometers.
5* Magnetization contrasts between anomalous body and surrounding rock in cgs units.

along two rift zones, one trending east and the other northwest.

The West Molokai shield is built up of basaltic lavas of the West Molokai series, and is cut by dikes which strike southwest.

MAGNETIC RELATIONS: Figures 10 and 24 indicate that two elements of the Molokai Fracture Zone cross the island. The North Molokai Primary Rift Zone anomaly (Fig. 24) defines here a bifurcation in the strike of the Molokai Fracture Zone. Along the northern shore of East Molokai, the rift zone defined strikes slightly south of west, whereas along the

northern shore of West Molokai, it strikes north of west. The Southwest Molokai Primary Rift Zone anomaly shows no change in east-west strike and appears to intersect the North Molokai Primary Rift Zone anomaly. This intersection occurs at the location of the North Molokai volcanic vent, which is defined geologically and topographically by a caldera.

Although there are numerous minor magnetic anomalies over Molokai (Fig. 25), five major anomalies define five major centers of intrusion. Two of these appear as broad anomalies on West Molokai and three as smaller an-

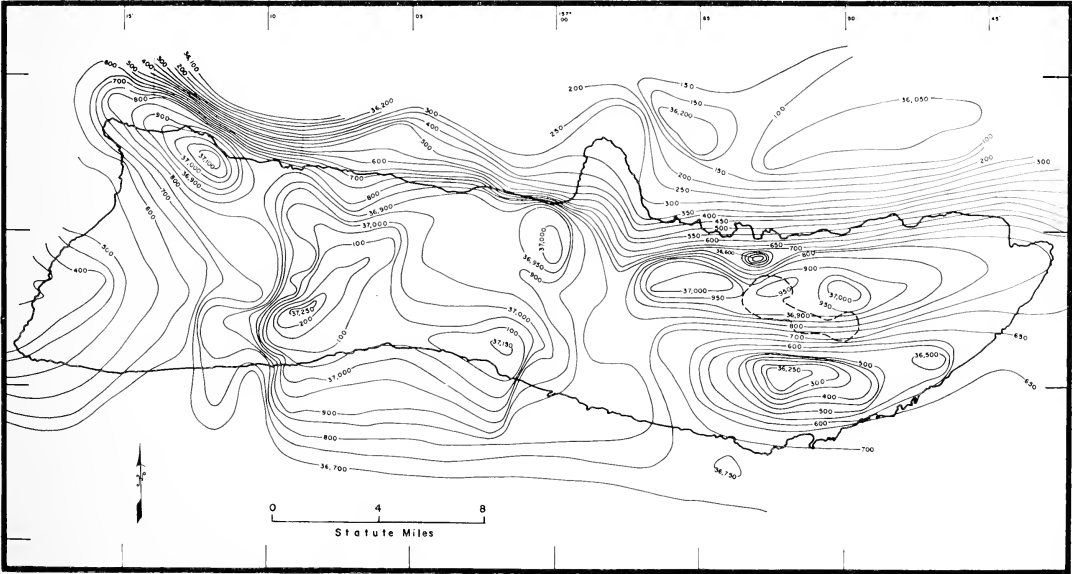


Fig. 25. Total force magnetic map of the island of Molokai, based on aeromagnetic profiles flown at 8,000 ft. Contour interval at 50 gammas.

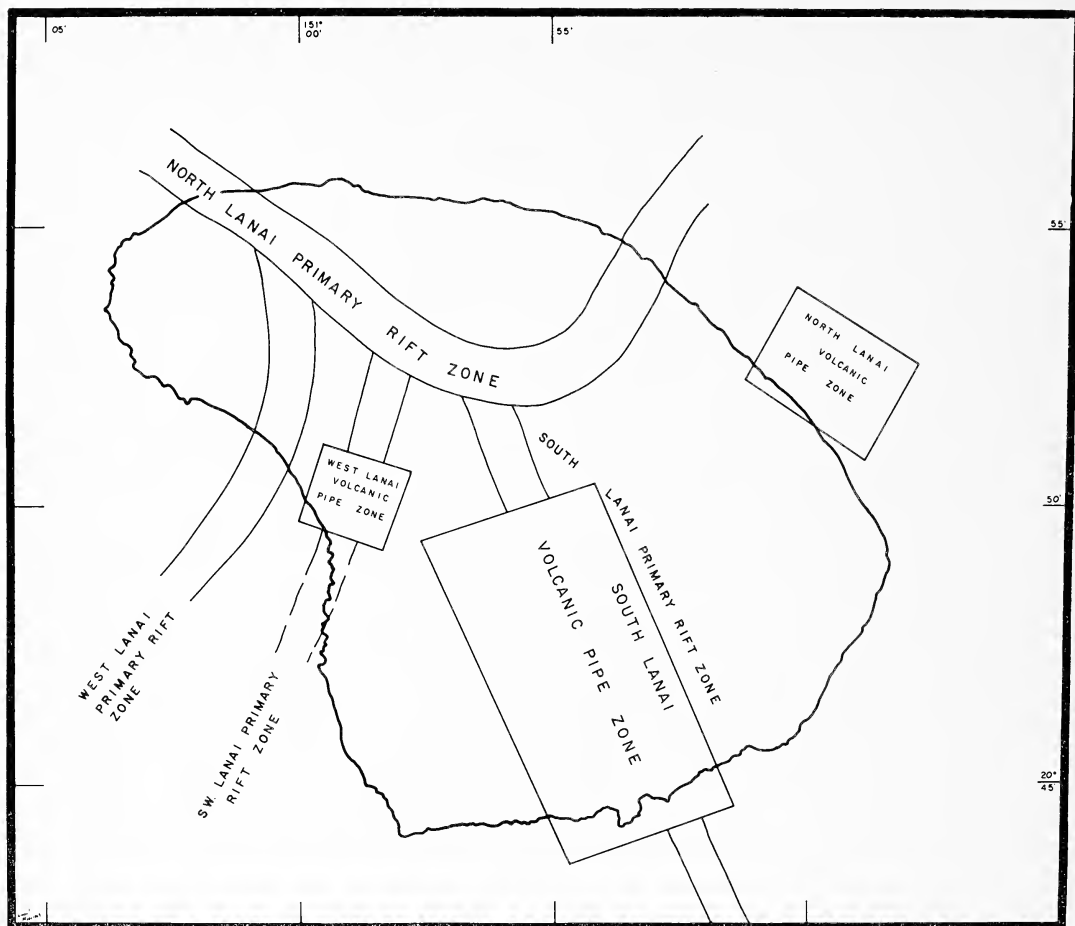


FIG. 26. Sketch of the primary rift zones and volcanic pipe zones of the island of Lanai.

omalies on East Molokai. The smaller anomalies appear to represent shallower sources which are superimposed upon the broad anomalies associated with the volcanic vent zone. These in turn are superimposed upon the primary rift trends believed to result from intrusions in crustal rifts. It appears, therefore, that East Molokai was formed by volcanic eruptions originating from at least two centers, and that West Molokai was formed by eruptions originating from at least three centers. The results for the analyses of the four principal magnetic anomalies are listed in Table 4.

In connection with the Southwest Molokai Volcanic Vent Zone, it is to be noted that the associated anomaly is inversely polarized. As explained in connection with relations on Maui, this can be explained as being due either to a reversal of the earth's magnetic field during the

period of solidification of magma within the vent, or to a filling of the vent with possibly olivine-rich rock which is less magnetic than the surrounding basalts. The computed magnetization contrast of 7.7×10^{-3} cgs units between the pipe zone rocks and the surrounding basalts is well within the range of possible magnetization contrast between olivine-rich basalt and tholeiitic basalt.

Island of Lanai

GEOLOGY: Lanai consists of a single shield-shaped volcano. According to Stearns (1940*b*), outpouring of lava has taken place from three sets of fissures that form three rift zones (Fig. 26), a northwest rift zone, a southwest rift zone, and a faulted south rift zone. Numerous dikes and faults occupy these rift zones. Basaltic flows erupted from these fissures and formed the

shield, and very little pyroclastic material appears to have been associated with the eruptions.

MAGNETIC RELATIONS: The three rift zones as described by Stearns are all reflected by magnetic anomalies (Fig. 27). Three major primary rift zone anomalies and two major volcanic vent zone anomalies are indicated. The prominent North Lanai Primary Rift Zone anomaly (Fig. 10) appears to be a member of the Molokai Fracture Zone system. The westward portion of the North Lanai Primary Rift Zone anomaly coincides with the Northwest Rift Zone of Stearns. Similarly, the South Lanai Primary Rift Zone anomaly coincides with the faulted South Rift Zone of Stearns. The West Lanai Primary Rift Zone has no apparent surface expression.

The South Lanai Volcanic Vent Zone anomaly, as elsewhere, probably reflects the intrusive rocks from which the majority of the lavas of Lanai originated. This vent zone is also marked by a pronounced gravity high. Though the geologic extent of the vent zone is broad (12 km long, 6.5 km wide) the total amplitude of the associated magnetic anomaly is low (150 gammas peak-to-peak). A depth analysis of this anomaly indicates that the top of the disturbing body lies at a depth of only about 0.8 km below the surface and appears to have a thickness of only about 2–5 km. The probable magnetization contrast with the surrounding basalts is low and of the order of $2.0\text{--}5.0 \times 10^{-3}$ cgs units.

Similarly, the magnetic anomalies designated as the West Lanai Volcanic Vent Zone and the

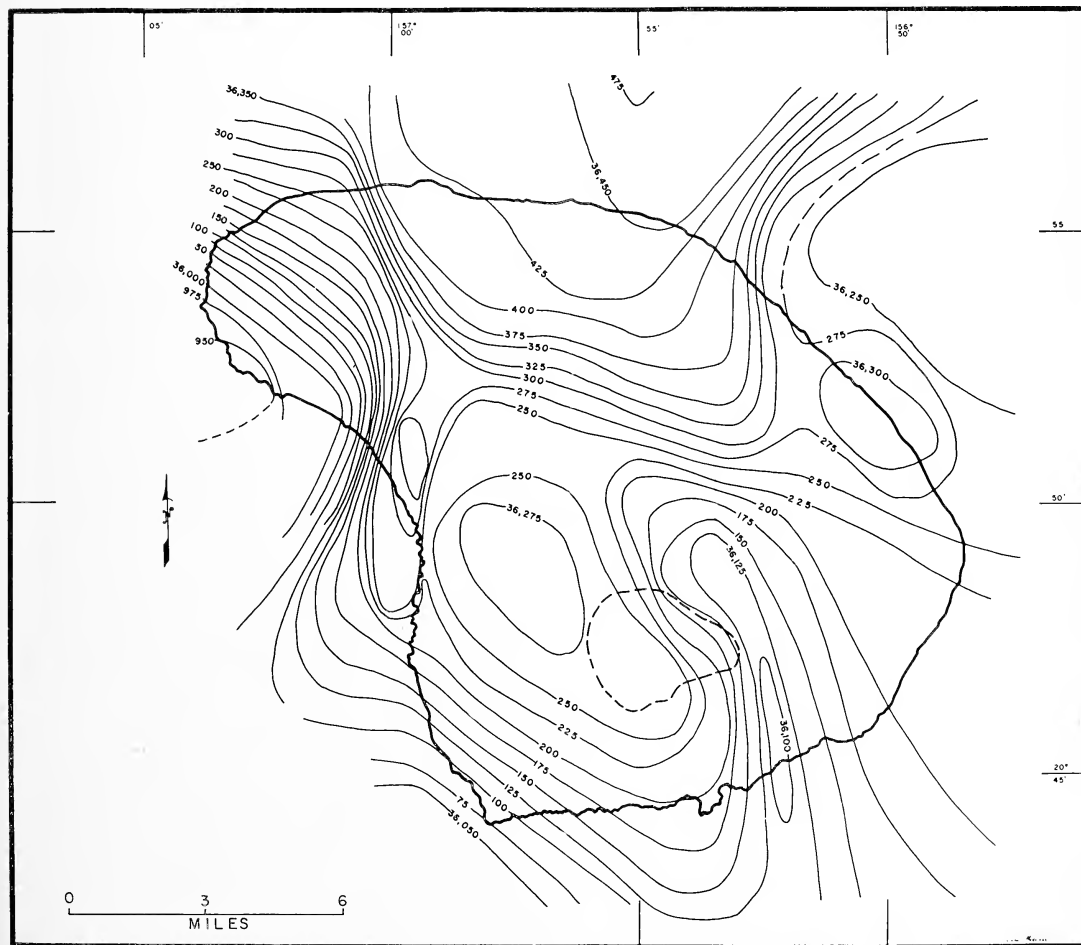


FIG. 27. Total force magnetic map of the island of Lanai, based on aeromagnetic profiles flown at 8,000 ft. Contour interval at 25 gammas.

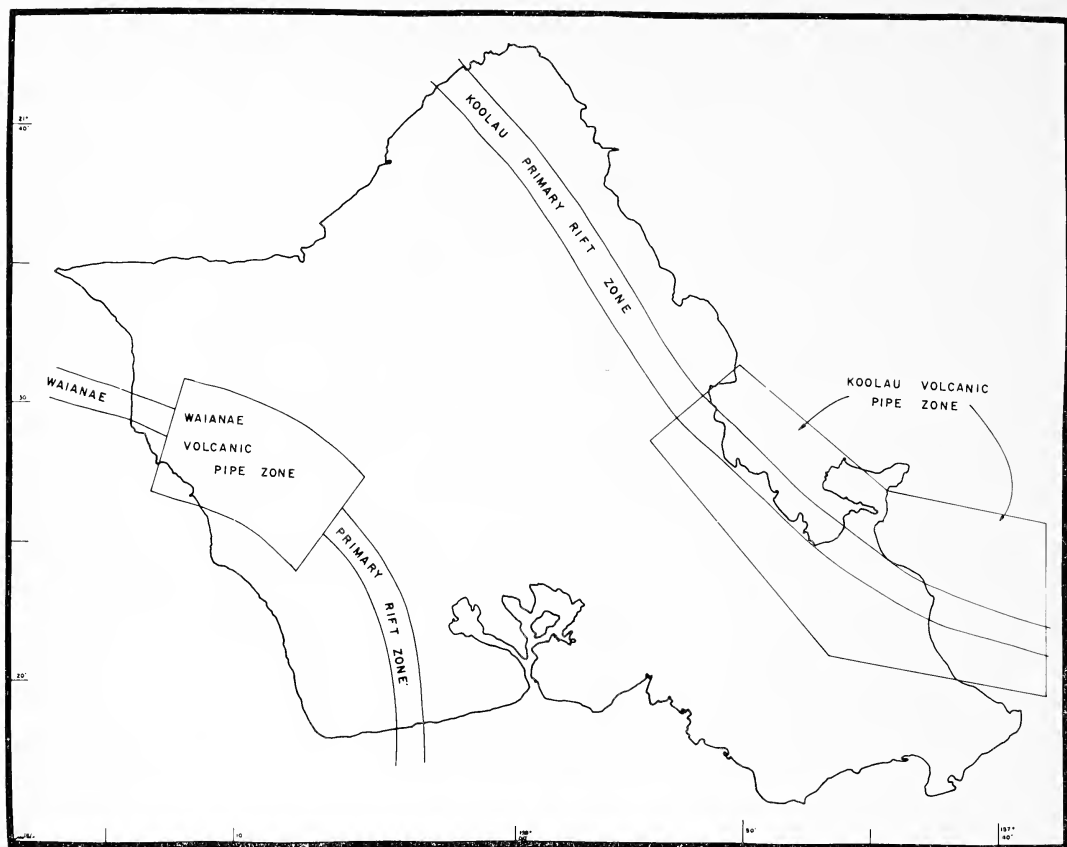


FIG. 28. Sketch of the primary rift zones and volcanic pipe zones of the island of Oahu.

North Lanai Volcanic Vent Zone are small in amplitude, 25 gammas for the former and 50 gammas for the latter. These two volcanic vent zones also probably represent shallow sources of volcanic activity. Geologically, the West Lanai Volcanic Zone is located in the area of the Southwest Rift Zone of Stearns (1940).

Island of Oahu

GEOLOGY AND GEOLOGIC STRUCTURE: Oahu was built by lavas erupted from two centers—the Waianae Volcano and the Koolau Volcano. Three groups of lavas form the Waianae volcanic range. The older lavas, probably of late Tertiary age, appear to be largely pahoehoe basalts, while the late stage eruptions produced large cinder cones and some alkalic basalts. The Waianae Volcano, like other Hawaiian volcanoes, produced only small amounts of ash, and the lavas were extruded both from a central vent and from fissures. Dikes and rifts are

numerous in the Waianae caldera and range in thickness from a few inches to several feet. Stearns (in Stearns and Vaksvik, 1935), after a study of the rift zones on Kilauea and Mauna Loa and in the Waianae caldera, noted that in almost all cases of rifting in the Hawaiian volcanoes the magma is confined to fissure zones that rise from the magma reservoir to the surface. Concentration of dike rocks in certain zones such as these probably could produce the elongate magnetic trends observed over such rift zones. Three dike systems have been mapped by Stearns (1939), and it will be seen that all of these rift zones lie within the boundaries of the Waianae Primary Rift Zone anomaly (Fig. 28). Furthermore, judging from the magnetic trend map of the seaward magnetic anomalies (Fig. 9), the Waianae Primary Rift Zone extends offshore west and south of Oahu.

The Koolau volcanic range is composed of the Koolau, Kailua, and Honolulu series. Both

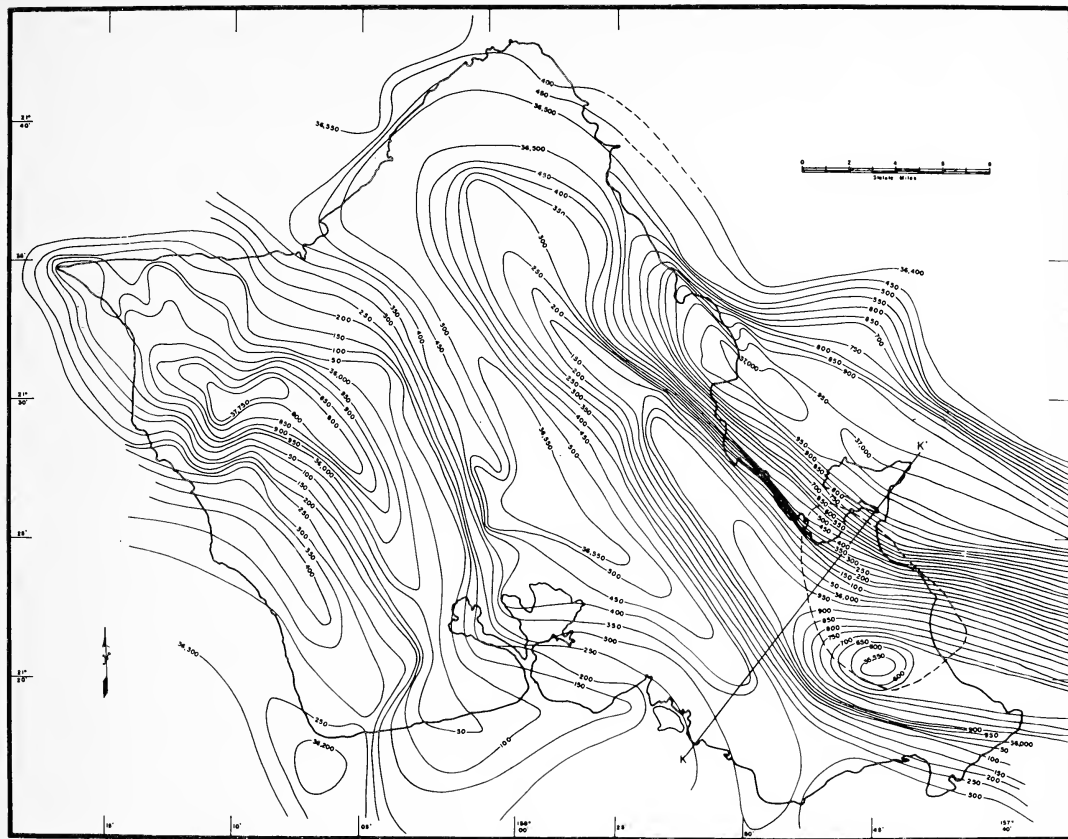


FIG. 29. Total force magnetic map of the island of Oahu, based on aeromagnetic profiles flown at 10,000 ft. Contour interval at 50 gammas.

the Koolau and Kailua series were erupted from the Koolau Volcano, and the Kailua series represents a hydrothermally altered intra-caldera group. Dikes are very common in the Kailua series, which occupies the Koolau caldera, and form a complex with younger dikes intruding into older ones. Many of the dike breccias and flows in the Koolau caldera are hydrothermally altered. It is believed that rocks of both the Kailua and Koolau volcanic series were erupted from the fissure zones of the Koolau Volcano. Fissure eruptions also characterized the building up of the Koolau volcanic shield. As in the Waianae area, the Koolau Primary Rift Zone anomaly (Fig. 28) coincides with the rift and dike zones of the Koolau Volcano, and, as with the Waianae Primary Rift Zone, is not confined by the shores of the island of Oahu.

MAGNETIC RELATIONS: The magnetic field of the island of Oahu (Fig. 29) is relatively sim-

ple. There are two primary rift zone anomalies, the Koolau and the Waianae, on each of which is located a large and distinct volcanic vent zone anomaly. These correlate with the Waianae and Koolau volcanic calderas. Both of these two volcanic centers are marked by distinct positive gravity anomalies (Woollard, 1951; Strange, 1964). However, the Koolau caldera, which is marked by a large amplitude 1,200-gamma peak-to-peak magnetic anomaly, is inversely polarized, whereas the Waianae caldera is marked by a 650-gamma, normally-polarized magnetic anomaly. The Koolau caldera has also been studied by seismic measurements (Adams and Furumoto, 1965; Furumoto et al., 1965), which show high velocity rock (7.5 km/sec) at a depth of only 1600 m.

Inasmuch as the Koolau caldera marks not only the site of one of the largest magnetic anomalies observed so far over the Hawaiian

Ridge, but also the only prominent magnetic anomaly which is inversely polarized, it is of special interest. This reversal in the magnetic field observed over the Koolau caldera can be explained either by the intrusion of weakly magnetized volcanic rocks within the Koolau Rift Zone or by a temporary reversal of the earth's magnetic field during the solidification of Koolau intrusive rocks. The explanation is not obvious, as studies of the extrusive rocks give conflicting data. The Honolulu series, for example, does not exhibit reversed magnetic polarization. Also, dike rocks collected within the Koolau caldera by the writers show normal directions of polarization in the laboratory. However, their intensities of remanent magnetization are lower than are those of the surrounding basalts. On the other hand, the results of polarization studies by McDougall and Talling (1963) indicate that the Koolau series of basalts are inversely polarized.

As the magnetic anomaly across the Koolau caldera (Fig. 3) shows that the point of inflection of the dipole is centered over the middle of the Koolau caldera, the inverse polarization is not a surficial effect but is one extending to depth. A gravity analysis (Strange, 1964) of the gravity high over the caldera requires a rock density of 3.2 gm/cc extending from a depth of 1 km to at least 16 km, and horizontal dimensions expanding with depth, as shown in Figure 3. This corroborates closely the seismic analysis by Adams and Furumoto (1965). The high seismic velocities and high densities suggest that the disturbing rock mass is a peridotite. However, it is not clear whether the inverse magnetic polarization is related to diamagnetism or to a past reversal in the earth's magnetic field. That the observed low susceptibilities for olivine-rich rocks could account for the anomaly is shown by the theoretical profile for a peridotite-filled caldera (Fig. 3): the computed profiles fit the observed profile within 50 gammas. A magnetization contrast of 15×10^{-3} cgs units would give excellent agreement between the observed and computed profiles. If this is the case, one then has to account for most other vent zones having the caldera "pipe" filled with highly magnetic rock having a susceptibility of approximately 2×10^{-3} cgs units. On a statistical basis, the diamagnetic explanation appears to be less reasonable than a reversal

in polarity. Only by drilling to the source rock, however, will the explanation be determined.

The geologic analysis of the Koolau Volcanic Vent Zone magnetic anomaly, on the basis that it is a ferromagnetic body inversely polarized, indicates that it is approximately 12 km wide at a depth of 1.6 km and extends to a depth of approximately 16 km. The intrusive rock having reversed polarity has a magnetic susceptibility of 20×10^{-3} cgs units.

The analysis of the magnetic field over the Waianae caldera shows that the Waianae Volcanic Vent Zone averages 9 km in width at a depth of 800 m and extends to a depth of 5 km. The rocks occupying the vent zone are normally polarized with a magnetization contrast of 9.0×10^{-3} cgs units.

Island of Kauai

GEOLOGY: According to Macdonald et al. (1960), Kauai is one of the oldest of the Hawaiian Islands. It consists principally of a shield volcano built up from the sea floor by innumerable eruptions of thin lava flows from a central vent and rift zones (Fig. 30). Activity started in the Kauai Volcano in early or middle Pliocene times. Growth of the shield was rapid and was completed before the end of the Pliocene. Towards the end of its growth, the summit of the shield collapsed and formed a large central caldera. A smaller caldera in the southeast portion of the island may or may not have had a contemporaneous origin. Later flows filled the grabens that formed after the caldera collapsed. The flows that built up the shield volcano as well as the later flows that filled the caldera are composed predominantly of olivine basalt.

Thus, the volcanic shield is made up of a basaltic sequence, termed the Waimea Canyon series, which is divided into four formations. The eastern part of the shield is veneered by later lavas of the Koloa series, which were erupted after a long period of erosion and continued through most of the Pleistocene epoch. Dikes occur in all the formations over most of the island with a dominant east-northeast trend (Macdonald et al., 1960). However, no well-developed dike complexes, like those found on the other islands, are observed.

MAGNETIC RELATIONS: The total intensity magnetic map of Kauai (Fig. 31) shows that

three major primary rift zone anomalies cross the island. These are designated in this paper as the North Kauai Primary Rift Zone, the Waimea Primary Rift Zone, and the Koloa Primary Rift Zone (Fig. 30). One volcanic vent zone is indicated on each of these primary rift zones. All three vent zones are normally polarized with maximum peak-to-peak amplitudes of the magnetic anomalies ranging from 300 gammas (North Kauai Volcanic Vent Zone), to 400 gammas (Waimea Volcanic Vent Zone), to 500 gammas (Koloa Volcanic Vent Zone). All three primary rift zones strike in a general westerly direction, converging towards the western portion of the island. It is significant that the Niihau Primary Rift Zone anomaly originating over the island of Niihau

converges with the Koloa Primary Rift Zone anomaly. This association suggests a common rift zone origin for the two islands—or, more likely, that Niihau was formed as a result of southward branching of the Koloa Primary Rift Zone. It is also significant that, as in all the Hawaiian Islands, the primary rift zones originate in the ocean and cross the island without interruption.

The Waimea Volcanic Vent Zone coincides with the magma conduit which is defined geologically and is believed to be the source for the lavas which built the Kauai shield. The geologic analysis indicates that the vent zone is approximately 11 km long and 6.5 km wide, with its upper surface buried about 1.6 km beneath the peak of Mt. Waialeale and its base

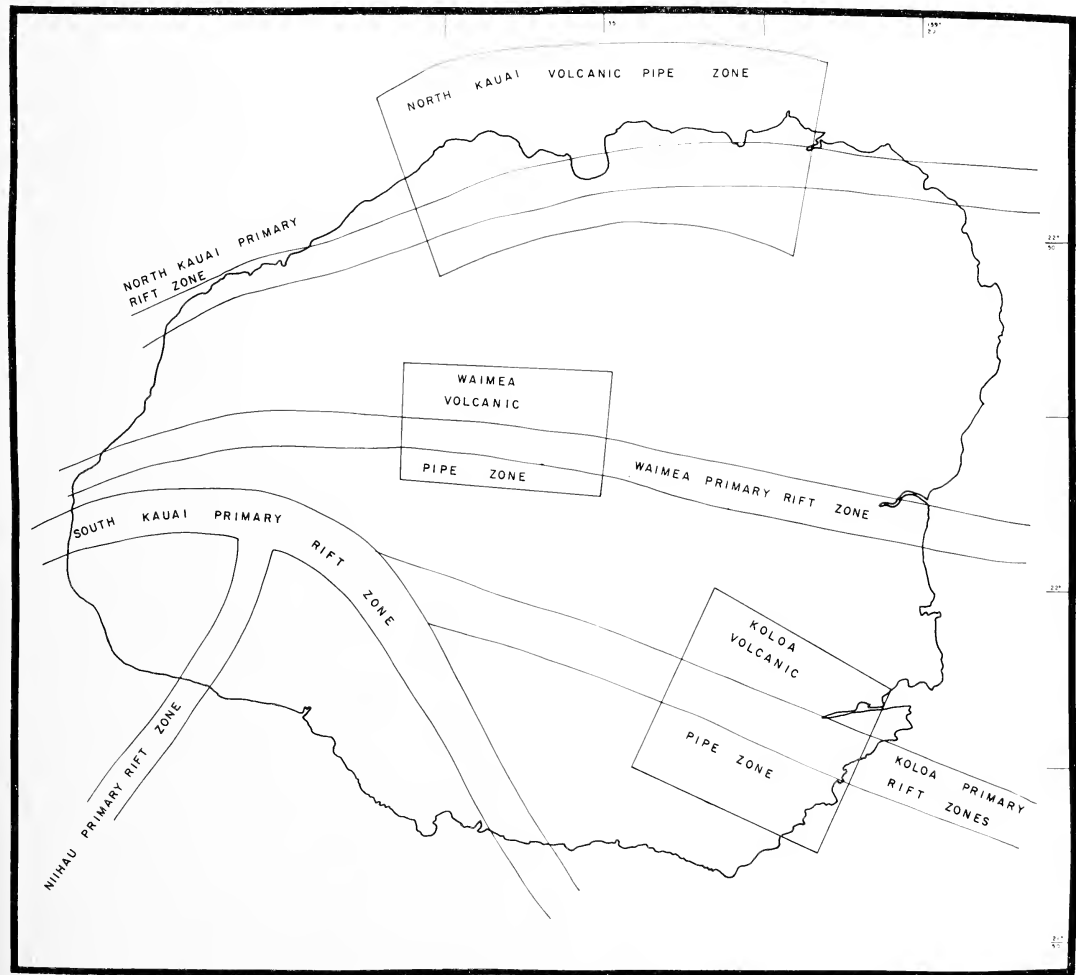


Fig. 30. Sketch of the primary rift zones and volcanic pipe zones of the island of Kauai.

Niihau originated. The dike zones mapped by Stearns on Niihau have the same strike as the Niihau Primary Rift Zone and the largest concentration of the dikes occurs within the boundaries of the trend.

The horizontal dimensions of the vent zone are 8 km by 8 km and the top surface of the anomalous body is located 0.8 km beneath the surface and its base at 6.0 km. The dike rocks that are exposed above the vent zone probably are representative of the anomalous volcanic rocks occurring within the deeper portions of the pipe zone. This conclusion stems from the apparent association between the Niihau dike

swarms and the Niihau Volcanic Vent Zone. Rocks within the vent area appear to have a magnetization contrast of 8.0×10^{-3} cgs units with the surrounding basalts.

CONCLUDING REMARKS

The airborne magnetic study reported here has shown that the area on and adjacent to the Hawaiian Islands is characterized by two types of magnetic anomalies: those that are elongated and extend for several tens of kilometers, and those that are centered over local areas. In all cases the local type anomalies are superimposed on the axes of the elongated type anomalies.

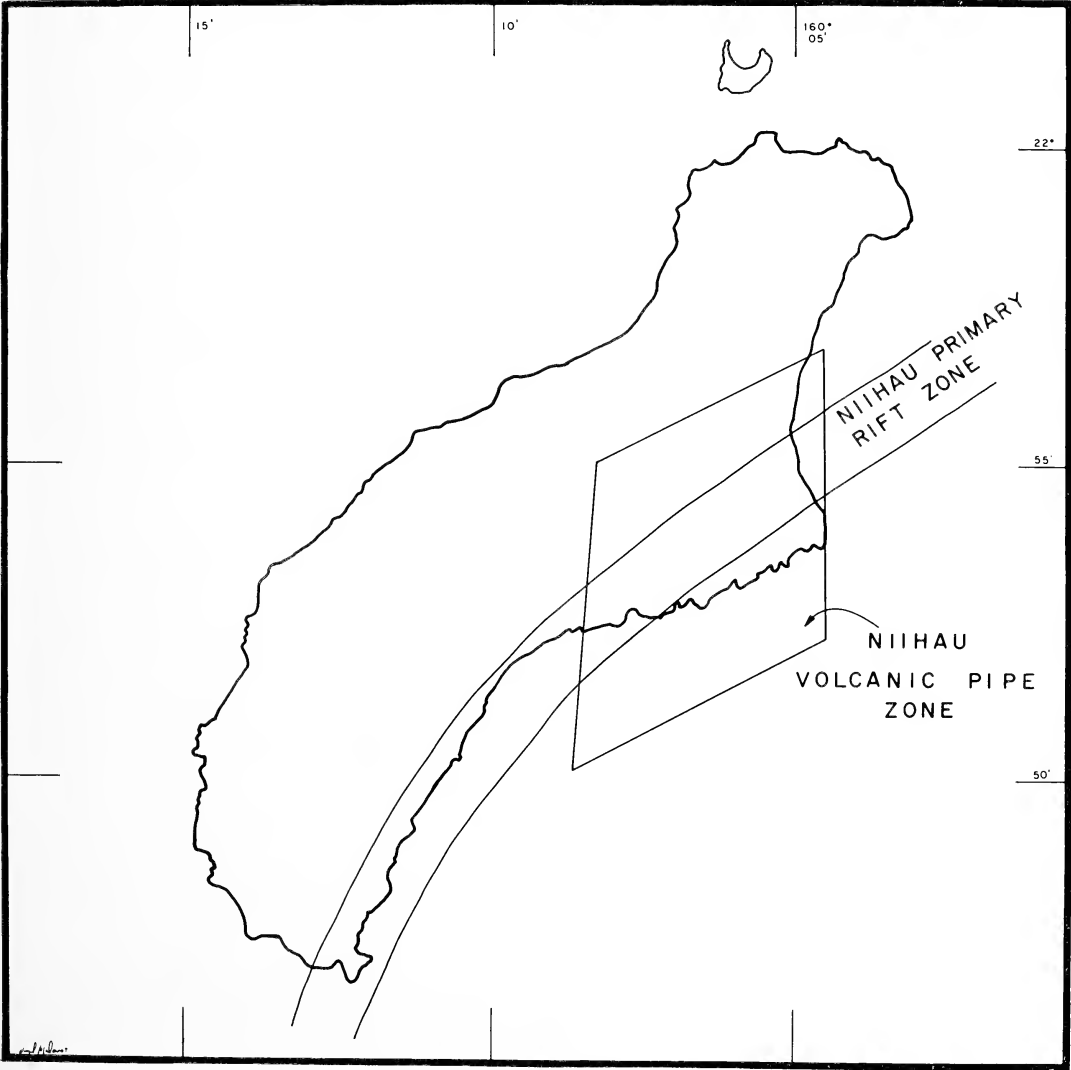


FIG. 32. Sketch of the primary rift zone and volcanic pipe zone of the island of Niihau.

Geologically, the local anomalies are associated with centers of volcanism, but most of the elongate anomalies do not have surface geologic counterparts and are believed to represent intrusions of mantle rock into rift type fractures in the upper mantle and overlying crust.

The majority of the prominent magnetic anomalies defining trends of crustal rifts strike

parallel to one of the two directions of the Hawaiian Ridge. One direction parallels the east-west strike of the Molokai Fracture Zone. The other direction parallels the west north-west-east southeast strike of the crest of the Hawaiian Ridge. Inasmuch as the trends parallel to the Hawaiian Ridge are truncated by those parallel to the Molokai Fracture Zone, the

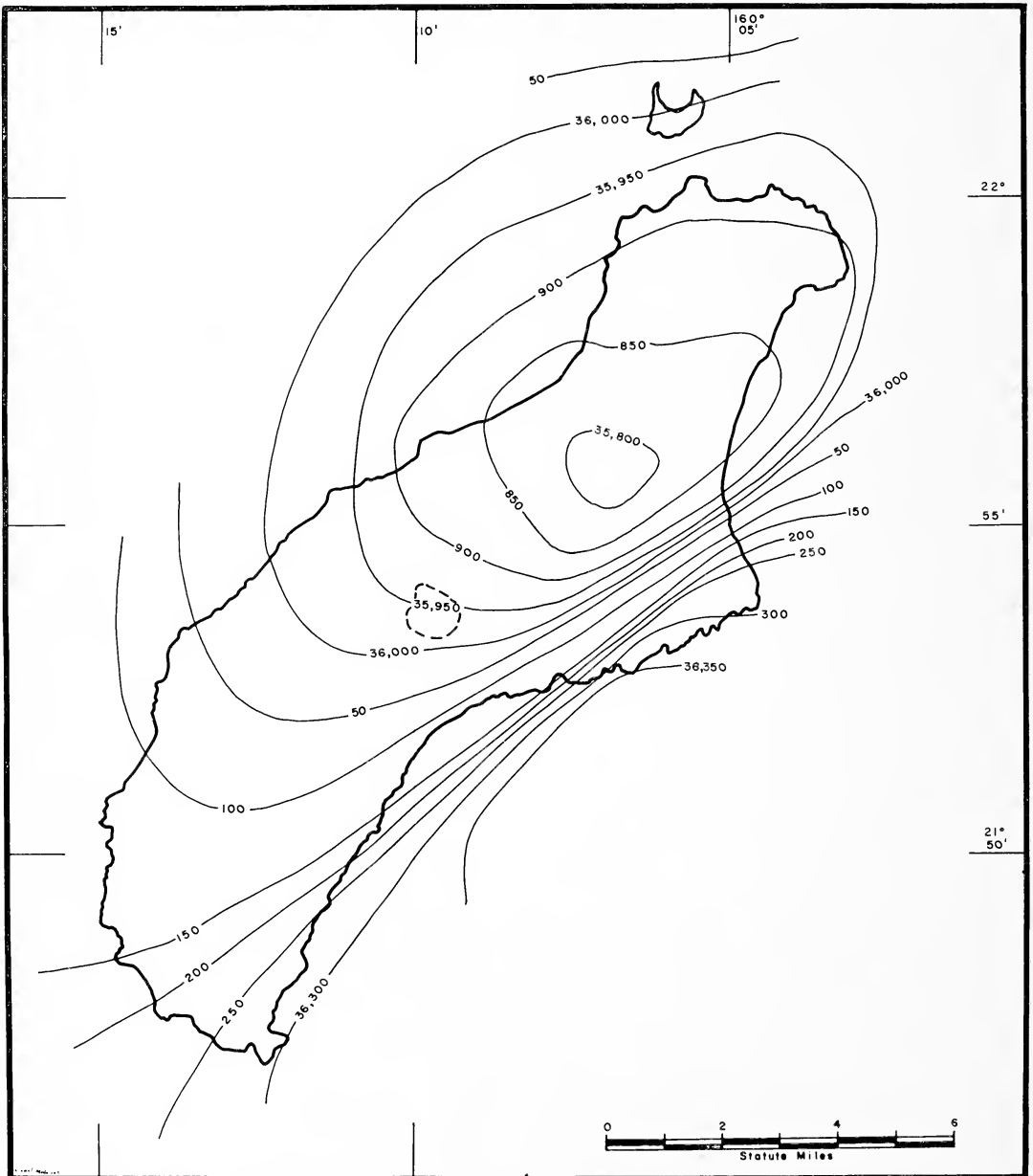


FIG. 33. Total force magnetic map of the island of Niihau, based on aeromagnetic profiles flown at 8,000 ft. Contour interval at 50 gammas.

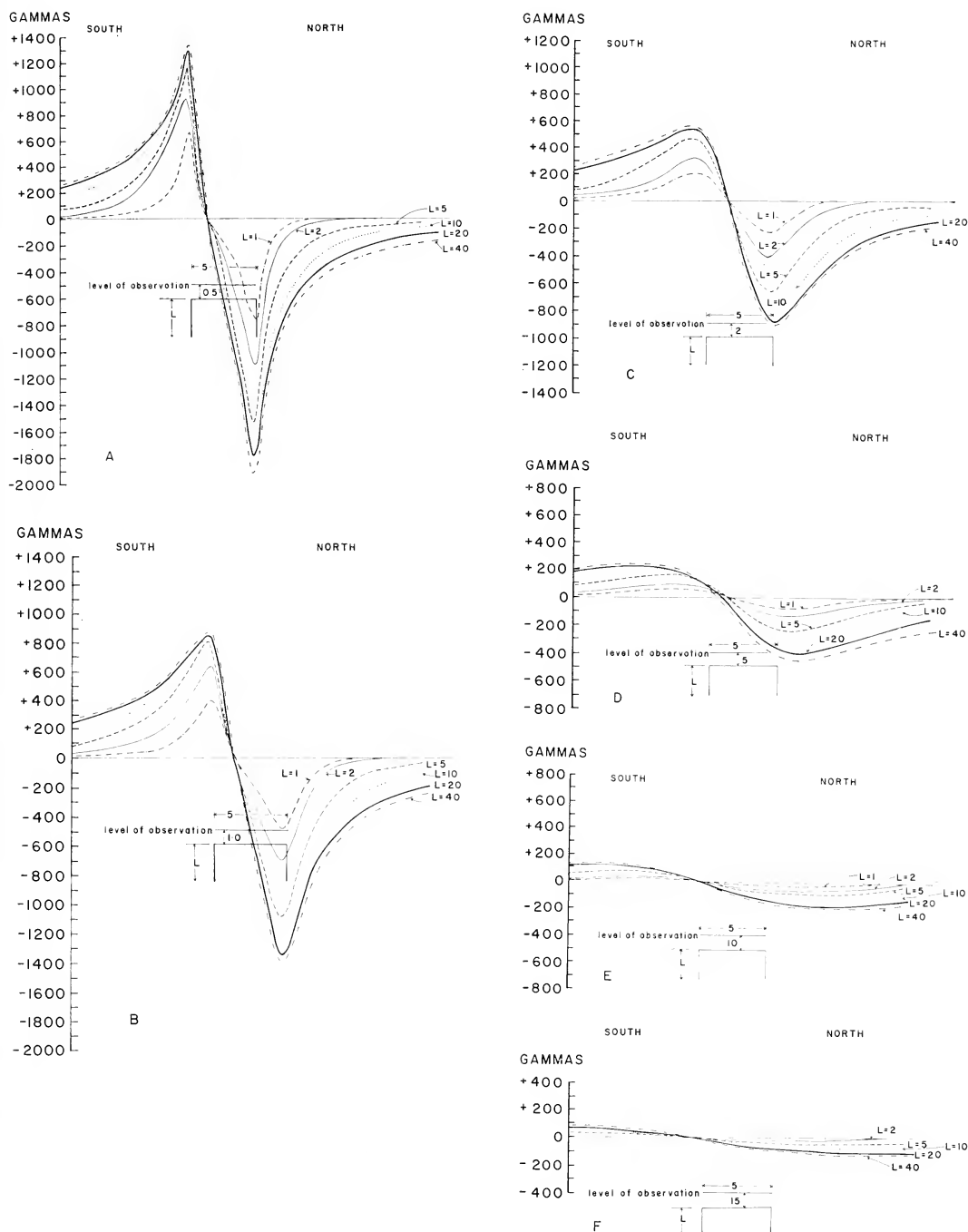


FIG. 34A-F. Magnetization of two-dimensional vertical bodies, where strike of profile = 0° ; inclination of earth's magnetic field = 35° ; total regional magnetic force = 36,000 gammas; susceptibility = 10.0×10^{-3} cgs units; and depth to top of body from level of observation = (A), 0.5 unit; (B), 1.0 unit; (C), 2.0 units; (D), 5.0 units; (E), 10.0 units; and (F), 15.0 units.

trends paralleling the Hawaiian Ridge probably are geologically older. Although data are available only for the eastern end of the Hawaiian Ridge, they support the concept of a progressive development of the Hawaiian Islands along a major fault or fracture zone. However, because the strike of east-west magnetic anomalies crosses the Hawaiian Ridge without interruption (Fig. 9), there is little question that the Molokai Fracture Zone has played an important role in the development of the islands lying east of Molokai. Certainly, some of the Hawaiian volcanoes appear to have formed where tectonic elements of the Molokai Fracture Zone have intersected with tectonic elements of the Hawaiian Ridge. All the magnetic anomalies on the islands of Hawaii, Maui, Kahoolawe, Molokai, Lanai, Oahu, Kauai, and Niihau apparently have developed from intrusions into crustal and upper mantle rift zones which are continuous for long distances.

Save for one major exception—the Koolau caldera anomaly on Oahu—most of the anomalies indicate normal polarization and the presence of intrusive rock similar to peridotite. In no case does the topographic effect bias the anomaly picture indicating that the anomaly control is from intrusives at depth.

Because of the consistency and the lack of any discordance in the magnetic anomalies, it is highly unlikely that the Hawaiian Ridge developed through any mechanism of horizontal drift of the crust from a single volcanic center, as was postulated by Wilson (1963).

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An Annotated Bibliography on North Pacific Albatrosses¹

HUBERT FRINGS, MABLE FRINGS, and CARL FRINGS²

THREE SPECIES of albatrosses (Family Diomedidae) are breeding residents in the North Pacific—Laysan Albatross (*Diomedea immutabilis*), Black-footed Albatross (*D. nigripes*), and Steller's or Short-tailed Albatross (*D. albatrus*). At various times each of these has been decimated by man, and for some time *D. albatrus* was believed to be extinct. Their fate is by no means certain now, and scientific interest in them is growing, particularly in the two species resident on the Leeward Islands of the Hawaiian chain (*D. immutabilis* and *D. nigripes*). In our own attempts to gather information on these birds from the literature we experienced great difficulty, for, while the total number of published articles and books is not too large, the bibliographies in published works are incomplete or inaccurate, and the papers are scattered in many journals. Accordingly, we have attempted to prepare a bibliography that is as complete as we can make it now. Each reference has been read, classified, and abstracted, and this publication embodies the results.

This bibliography does not represent all of the literature on the North Pacific albatrosses, but we believe it includes all major works. We have a few incomplete references which we have been unable to verify or identify as yet. When found these will be read and abstracted. Also other references may turn up or be called to our attention. We hope to be able to publish these, as soon as all are found, in a supplement.

The bibliography is arranged alphabetically and chronologically by first author. This is followed by a combined taxonomic and subject index. Each reference, besides containing the

usual information, is followed by a group of symbols within parentheses forming a symbolic abstract, and by a brief statement of contents. Since many longer works deal with more than just these birds, relevant pages of larger papers are given; this should be useful for persons wishing to order photocopies.

The following sample references illustrate the system used in this bibliography:

Kaeding, Henry B. 1905. Birds from the West Coast of Lower California and adjacent islands. *Condor* 7:105–111. (Tech.; nig., imm.; Dist., Ecol.) Sighting records with notes on seasonal variation in numbers (p. 107).

Hattori, Toru. 1889. (The story of the Albatross of Torishima.) [In Japanese.] *Zool. Mag. (Dobutsugaku Zasshi)*, Tokyo 1(12):405–411. (Tech.; alb.; Gen.) Austin (1949): general work on behavior, reproduction, and habits.

The first of the symbols within the parentheses, before the semicolon, indicates the level of writing of the author. The four designations used are:

Tech.: technical, scholarly, scientific presentation

S. Tech.: semitechnical, scholarly, but less formal and more anecdotal

S. Pop.: semipopular, written for the educated layman, with few technical terms

Pop.: popular, entirely nontechnical

These classifications imply no judgment of the validity of the information presented; popular articles, for instance, may be of great value for certain studies.

Next, followed by a second semicolon, are the species discussed:

nig.: *D. nigripes*

imm.: *D. immutabilis*

alb.: *D. albatrus*

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The last part of the material within the parentheses gives the subject categories discussed. If five or more of the subject categories are covered for one species, the article is termed general (Gen.). The following are the subject headings used:

- Desc.: description, taxonomy, and coloration
- Dist.: geographical distribution
- Morph.: morphology and measurements
- Phys.: physiology
- Behav.: behavior, social and sexual habits, communication, flight, etc.
- Repr.: reproduction, nesting, life cycles, egg descriptions, embryology, development of young
- Ecol.: ecology, populations, food, inter-specific relationships
- Prac.: practical relations with man, depredations by man, captivity, bird-strike problem

Following the symbolic abstract is a sentence giving information about the work not obvious from the abstract, or further characterizing it. This sentence is followed, in some cases, by page numbers in parentheses. These are the pages on which information about albatrosses is found.

Now we may interpret the Kaeding reference. It is a technical publication about both Black-footed and Laysan Albatrosses, dealing with their distribution and ecology, particularly as noted in the short statement. The relevant page in this article is 107.

The second illustrative reference shows some other points. The title is in parentheses, meaning that it is a translation of the original Japanese. At the beginning of the sentence is the notation: Austin (1949); this means that we did not read the work, but take the information from Austin's article. The only other secondary source used was that of Baker (1951).

The bibliography is followed by an index arranged by species, and under each, by subject headings, which are the same as those listed above. The symbolic abstract shows the largest number of subjects for all the species. In the index, on the other hand, only relevant subject references are listed for each species. For ex-

ample, in the Kaeding reference above, distribution is discussed for both *D. nigripes* and *D. immutabilis*, but ecology only for the former. Therefore, in the index the reference is not listed under ecology for the Laysan Albatross. Thus, if one wishes to know whether a reference has information on a specific subject listed in the symbolic abstract for a particular species, he can determine this from the index.

In some of the older articles modern names were not used, and interpretation was necessary. In a few cases it was impossible to tell which species was meant. In such cases, a question mark is placed after the species symbol, indicating that the species listed is our best guess.

We would like to express our appreciation to Mildred Arinoki for her conscientious work on typing and checking the manuscript.

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Observations on the Ecology of Four Apogonid Fishes

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THE FISHES of the family Apogonidae are small, inconspicuous creatures which live in and around coral reefs. In the atolls of the central Pacific they are common, occasionally colorful, and sometimes occupants of specialized habitats. This paper reports aspects of the ecology of four species which are uncommon in collections: *Apogon novaeguineae* Valenciennes, which lives among the spines of the sea urchin *Echinothrix diadema* (Linnaeus); *Apogon leptacanthus* Bleeker, which occurs in vast shoals associated with the coral *Montipora gaimardi* Bernard; and *Apogon gracilis* (Bleeker) and *Gymnapogon gracilicauda* Lachner, which school in open water over reefs. Observations were made in the Marshall Islands during the summers of 1950, 1951, and 1955, when the writer participated in research projects sponsored by the Office of Naval Research, the University of Hawaii, and the Pacific Science Board of the National Research Council. Thanks are due these institutions as well as to the Military Air Transport Service and the Atomic Energy Commission who supplied transportation and many facilities. I also wish to thank Mme. I. Catala (Noumea Aquarium, New Caledonia), Dr. D. B. E. Magnus (Zoologisches Institut, Darmstadt, Germany), Dr. C. L. Smith (American Museum of Natural History, New York), Dr. R. A. Stevenson (University of Puerto Rico), and Mr. G. P. Whitley (Australian Museum, Sydney) for supplemental data.

Apogon novaeguineae Valenciennes

Visits were made to a number of atolls in the Marshall and Gilbert groups, but *A. novaeguineae* was found only at Eniwetok in the northern Marshalls. Here it occurred in the lagoon off Parry and Japtan Islands, and on the shallow ocean reef northwest of Cochiti Island. The fish was seen on 33 occasions, 23 times

among the spines of the poisonous sea urchin *Echinothrix diadema*, and 10 times nowhere near an urchin. Both the fish and urchins lived in caves or beneath ledges, neither occurring in less than 4-ft depths and most living between about 8 and 18 ft. The number of fish per urchin ranged from 3 to 12, with 4 or 5 being usual.

Another apogonid, *Paramia quinquelineata* (Cuvier) sometimes accompanied *A. novaeguineae* among the urchin spines, while several other species were found in urchins lacking *novaeguineae*. These were *Apogon fraenatus* Valenciennes, *Apogon savayensis* Günther, *Apogon novemfasciatus* Cuvier, and the pipefish *Doryrhamphus m. melanopleura* (Bleeker). The occurrence of these four fishes among urchin spines was uncommon and usually involved only one or two individuals in a particular urchin. The attitude of these spine-dwelling species was horizontal except for *Doryrhamphus*, which oriented parallel to the nearest spines with its head toward the urchin's test.

Most of the above spine-dwelling fishes bear lengthwise stripes, the exception being *A. savayensis*. This is a drab species which neither matches nor contrasts with the urchin and probably occurs among its spines only occasionally. *A. novaeguineae*, on the other hand, is one of the most brightly colored apogonids, and its brilliant yellow contrasts vividly with the black or deep red of the urchin.² Its stripes are in-

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² A description of the color of living *novaeguineae* could not be found in the literature and therefore is presented here. Ground color of body light yellow, with gold and silver iridescence on sides of head and trunk. Throat and gill membranes white, rest of head yellow with scattered dusky pigment, giving it a dirty appearance. Five narrow white lines on head and body: first from occiput to first dorsal, where it bifurcates and runs along dorsal bases to caudal peduncle; second from interorbital along top of head and trunk parallel to first, uniting with its mate on dorsal edge of caudal peduncle; third from tip of snout across iris,

conspicuous and in no way tend to camouflage the fish.

A number of other fishes have been reported to inhabit sea urchin spines. Most of these bear contrasting stripes or bars which may match the spines in size and color. Such ecological situations have been found elsewhere in the Apogonidae (Abel, 1960a:482, 1960b:34; Lachner, 1955:43; and Magnus, in press), Gobiesocidae (Briggs, 1955:141; Mortensen, 1940:250; and Pfaff, 1942:413), Centriscidae (Davenport, 1955:37; Herald, 1961:151; and Le Danois et al., 1957:121), and the sciaenid *Eques*, the clinid *Malacoctenus aurolineatus*, the gobiids *Gobiosoma multifasciatum* and *G. novemlineatum*, and the gobiesocid *Acyrtus rubiginosus* (C. L. Smith, personal communication).

Some spine dwellers match the urchin's color but lack stripes. These include the apogonids *Siphamia zaribae* (Whitley, 1959:16), *S. versicolor* (Eibl-Eibesfeldt, 1961:57), several species of the gobiesocid genus *Arbacia* (Jordan and Evermann, 1898:2340-2343), some specimens of the gobiesocid *Acyrtus rubiginosus* (C. L. Smith, personal communication), and the Hawaiian pomacentrid *Dascyllus albisella* (R. A. Stevenson, personal communication). Of these, *S. versicolor*, at least, has a changeable color pattern which includes a striped phase. Peculiarly enough, its stripes appear only when the fish is away from its urchin host (Eibl-Eibesfeldt, 1961:58).

Some of the authors mentioned above state that spine dwellers should align their stripes with the spines if their color pattern is to provide an effective camouflage. Apparently this is done by *Paramia bipunctata*, *Aeoliscus*, *Doryrhamphus*, and possibly *Diademichthys*. These fishes are thus protected not only by the physical barrier of the spines, but also by the visual barrier of their camouflage. Such a dual safeguard may be necessary if their predators are capable of probing between the spines for food.

touching upper edge of pupil, thence across midsides to caudal base; fourth from upper lip across iris, touching lower edge of pupil, thence across midsides to end of trunk; fifth from lower lip across suborbital to rear edge of opercle. Lines iridescent blue-white on head but faintly dusky on body. Tip of snout and lips sometimes red-orange. Iris yellow. Pectorals pale, other fins light red.

The other spine dwellers remain essentially horizontal, and their stripes are usually not aligned with spines. Obviously they are not camouflaged in this position, although the criss-cross pattern of lines thus presented may disrupt the fish's outline. It is also possible that color and pattern are of little consequence once the fish is within the spine shelter. Certainly its brilliant yellow color is a blatant advertisement for *A. novaeguineae*.

A few observations were made on *A. novaeguineae* repopulation following departure of the fish from their urchin host. One urchin was removed from its cave and placed on open bottom 4 ft in front of the cave's mouth. A ridge on the bottom prevented the urchin from being seen from the cave. As soon as their host was disturbed, the *novaeguineae* left it and took shelter among the spines of a second urchin in the cave. The exposed urchin was watched for 15 minutes but no fish left the cave to join it. The urchin was then lifted over the ridge and placed 3 ft in front of the cave's mouth. In 2 minutes a single *novaeguineae* swam to the urchin and settled among its spines, followed by a second fish a few minutes later. The urchin crept to the cave's mouth during the succeeding 10 minutes, without being joined by additional fish. Two more *novaeguineae* joined it just as it crossed the cave's threshold. The balance of its original population of fish remained with the second urchin during an additional 5 minutes of observation.

On June 18, 1955, an isolated coral mound containing four large *Echinothrix*, each bearing several *A. novaeguineae*, was heavily treated with rotenone and all of the *novaeguineae* collected. This mound was visited regularly for several weeks, and then less frequently. No *novaeguineae* had returned by July 12, but there were a number of them among the spines of one urchin on August 24. This indicates that *novaeguineae* is rather restrictive in its movements. Unfortunately the distance to the next aggregation was not recorded.

Ten of the rotenoned specimens were examined for food consumed. Of these, two fish were empty and three others (males) had their stomachs packed with embryonated eggs. Probably these fish had been brooding eggs in their mouths and swallowed them under duress. Of

the five with food in their stomachs, four contained callianassid-like burrowing shrimp, two had ordinary shrimp, one a crab, one contained mysids, and one an unidentified crustacean. Additional food items have been reported by Hiatt and Strasburg (1960:80). None of these food organisms seemed to be an urchin commensal, and therefore it is probable that the fish left their spine shelters to feed. This is not necessary for all spine dwellers, as illustrated by Pfaff's observations (1942:416) of *Diadema* feeding on the tube feet of *Diadema* and on the sessile eggs of a shrimp living among the spines. Rivero (1950:115) mentions but does not name certain inquilinistic fishes which feed on colonial hydroids and other invertebrates living on sea urchins, and Eibl-Eibesfeldt (1961:57) describes *Siphamia versicolor* picking at and probably cleaning the test of *Diadema*, which had previously inclined its spines in a possible cleaning posture.

Apogon leptacanthus Bleeker

A. leptacanthus was found at only one locale, the lagoon side of Uliga Island, Majuro Atoll, Marshall Islands. This apogonid was always associated with the low branching coral *Montipora gaimardi* Bernard. Large growths of *M. gaimardi* were conspicuous at the swimming beach near the Uliga airstrip, and much smaller patches were seen near the Uliga causeway. The water depth over these reefs was 2–6 ft. The fish occurred in sheetlike schools, one or two fish deep, which drifted about 1 ft above the *Montipora* branches. On the approach of a swimmer the school gently subsided into the coral, to emerge after his departure.

The most impressive features of the *A. leptacanthus* schools were the large numbers of individuals and the fact that the environment was quite different from the open-water situation in which schooling usually occurs. The largest school seen was found over a rectangular patch of *Montipora* measuring 60 by 80 ft. About half of this rectangle was occupied by the school, which contained 10–25 fish per sq ft according to numerous estimates. These figures give a school abundance estimate of 24,000–60,000 fish, certainly a remarkable concentration for any reef species. The number of fish in two other schools was estimated in the same

way; one contained 2,000–5,000 fish, and the other 500–1,250 fish.

Part of one of the *Montipora* beds was treated with rotenone to determine which other fishes coexisted with such dense concentrations of a single species. The only other fish which could be termed common was *Apogon snyderi* Jordan and Evermann. The following were taken in small numbers: *Chaetodon auriga* Forskål, *C. trifasciatus* Mungo Park, *C. lineolatus* Cuvier, *Thalassoma quinquevittata* (Lay and Bennett), *T. hardwickei* (Bennett), *Holocentrus laevis* Günther, *Parupeneus trifasciatus* (Lacépède), *Plesiops melas* Bleeker, *Ctenochaetus striatus* (Quoy and Gaimard), *Dascyllus aruanus* (Linnaeus), *Abudefduf glaucus* (Cuvier), *Amphiprion melanopus* Bleeker, and *Corythoichthys* and *Gymnothorax* juveniles too small to identify. Such a fauna is typical of most Marshallese coral communities except that here all individuals were small, most being the young of moderate-sized reef fishes. The dense forest of coral branches probably served as a protected nursery area for these small fishes.

The *Montipora* beds were visited on several occasions in 1950, 1951, and 1955. The *A. leptacanthus* schools were always present and, in fact, were regarded as permanent features by Uliga residents. Obviously the nutritional needs of this large population were great. The stomach contents of four rotenoned *leptacanthus* were examined, and revealed their principal food to be crustacean plankters, mostly crab zoea. Presumably these were obtained while the fish drifted above the coral. No *leptacanthus* were seen to feed, but all were noted to head in the same direction, and were probably exhibiting rheotactic rather than schooling behavior. Currents very probably convey planktonic food to the relatively stationary fish.

A brief color description of *A. leptacanthus* follows: ground color translucent olive-tan, traces of dusky pigment on snout. Iris, suborbital and supraorbital regions iridescent sapphire. Two short diagonal orange bars behind eye, two short vertical orange bars on opercle, and two more on sides above pectorals. A narrow yellow-white line on dorsal midline behind soft dorsal. Pelvics and pectorals reddish, anal with a basal red band and reddish rays. Soft dorsal and caudal rays are faintly reddish.

Apogon gracilis (Bleeker) and *Gymnapogon gracilicauda* Lachner

Unlike most Apogonidae, which dwell in close proximity to a sheltering substratum, *A. gracilis* and *G. gracilicauda* are apparently pelagic species. They were observed many times in the lagoon at Parry Island, Eniwetok Atoll, swimming in large, loose schools. Most schools were in the general vicinity of coral mounds at depths of 12–25 ft, but a few occurred over relatively featureless sand or coral rubble at the same depth. The *gracilis* schools were composed of several hundred individuals, whereas the *gracilicauda* schools were much smaller, consisting of perhaps 5–25 fish. The number of schools and the number of fish per school increased with the distance from shore.

Both fish were difficult to recognize as apogonids in life. Their pelagic occurrence was unexpected and their colorless glassy transparency made them hard to detect and characterize. The two could be told apart by the presence in *A. gracilis* of an internal black spot on the lower caudal peduncle and the black tip of its upper caudal lobe.

Morphologically, *Gymnapogon* is quite distinct from the rest of the Apogonidae and it is not surprising to find it occupying a different habitat. A summary of its physical peculiarities and their systematic significance has been presented by Lachner (1953:490). *Apogon gracilis*, on the other hand, is a typical apogonid and shows no particular adaptations to a pelagic mode of life (except possibly for its colorless transparency). The diet of four rotenoned *A. gracilis* consisted of pelagic crustaceans, mostly amphipods.

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Records of Asian and Western Pacific Marine Algae, Particularly Algae from Indonesia and the Philippines

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THIRTY YEARS AGO the marine algal flora of the Philippines was practically unknown. Records of the occurrence of several species have existed, of course, from the time of Blanco (1837) onward, but they are few in number and can hardly be accepted as equivalent to current critical identifications. Strongly pressed by the late Professor H. H. Bartlett, a devoted promoter of Philippine botanical exploration and research, the present writer began the assembly of materials available in the herbaria in the United States, notably at the University of California at Berkeley. Of these the collections of the late Professor W. A. Setchell, partly determined by him, were an important part. Much material was collected on request by correspondents in the Philippines, particularly by Professors Bartlett and G. T. Velasquez, and their assistants.

For the identification of this material the descriptions by Mme. Anna Weber-van Bosse and her collaborators in the "Siboga" reports were the best available; so materials from Java were secured for comparison. Support for the study of this rich accumulation was not continuous, and other major opportunities with support came about, and so the writer's personal participation in the project languished. The project was not altogether abandoned, however. A general account of the Chlorophyceae has appeared (Gilbert, 1942, 1943, 1946, 1947, 1961), together with a brief outline of the history of algal work in the area. The Halimedes were revised in a general study of that genus (Hillis, 1959), the Padinas similarly (Thivy, 1945, *inedit.*), the Turbinarias and a few other genera studied (Taylor, 1961, 1962, 1964, 1966 in press). Significant publication has come from the University of the Philippines (Velasquez, 1952, 1957, and several papers on Myxophyceae). A number of determinations,

particularly in *Chaetomorpha*, were originally made by Professor A. J. Bernatowicz. Likewise, many specimens collected by Dr. D. P. Abbott were determined by Dr. I. A. Abbott. The writer has again been able to devote time to determining this material, and it is proposed to give here a supplementary account of Chlorophyceae and of Phaeophyceae from localities not reported earlier. This is not intended to be a complete list of all species in these groups, for some of the records published earlier could not be confirmed.

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EXPLANATION OF TREATMENT

Because of the many station records offered here, an explanation of the pattern of treatment is in order. Since a great proportion of the specimens are in the herbarium of the University of California at Berkeley, only nonconforming cases are noted. The dates given are of the 20th century unless otherwise stated fully.

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Collector's initials may be ascertained from the list given below. Troublesome as it is to establish a system, papers in which localities are not treated in any geographic order are all but useless to the phyto-geographer. Here stations are cited from the Philippines southward and eastward in the northern hemisphere and then from Malaya eastward in the southern. Islands of archipelagos are generally listed from north to south, provinces and stations clockwise from the north around them. Great difficulty was met in dealing with station names from several languages or dialects, often recorded phonetically. An effort has been made to secure conformity and proper sequence, using in particular the map of the Philippine Republic issued by the J. P. Juan Co. of Ermita, Manila (1960), to some extent the maps of the United States War Department Corps of Engineers 1:50,000 series issued about 1945, and especially the gazetteers of the United States Board on Geographical Names. Considerably less satisfaction was achieved with respect to Indonesian localities.

The chief collectors were: Abbott, D. P.; Alcasid, G. L.; Balhani (Moro fisherman); Bano, G. E.; Bartlett, H. H.; Birtwhistle, W.; Blanco, G. J.; Christopherson, E.; Clemens, M. J.; Collado, E. G.; Copeland, E. B.; Corner, E. J. H.; Crus, M. T.; Curran, H. M.; Edaño, G.; Erlanson, E. W.; Fénix, E.; Fosberg, F. R.; Guitierrez, E.; Henderson, M. R.; Janaki-Ammal, E. K.; Keefe, A. M.; Kienholz, R.; Kostermans, A. J.; Kruckeberg, A. R.; Manacop, P. R.; Mangubat, L.; McGregor, R. C.; McKern, W. C.; Medina, E.; Merrill, E. D.; Metraux, E. M.; Möller, H.; Moore, G. C.; Newhall, P. M.; Nur, M.; Oie Yong Seng; Pullai, R. S.; Quisumbing, E.; Radin, R.; Ramirez n.n.; Ramos, M.; Robinson, C. B.; Rosario, F. del; Santos, J. V.; Setchell, W. A. (often with C. B. Setchell); Shaw, W. R.; Vasconcellos, M.; Vatter, A. E., Jr.; Velasco, D.; Velasquez, G. T.; Vivas, F.; Yates, H. S.

CHLOROPHYCEAE

ULVALES

ULVACEAE

Enteromorpha Link, 1820*Enteromorpha flexuosa* (Wulf.) J. Ag.

PHILIPPINES. Batanes Pr., Batan I., McGregor, vi 07. Luzon I.: Cagayan Pr., Calayan I., McGregor P43, 03, Gonzaga, Edaño 77293, 94, x 29; Quezon Pr., Tualog, Ramos and Edaño 29165, v 17; Rizal Pr., Malata, McGregor, 14 i 05; Ilocos Sur Pr., Magsingal, Collado 9, vi 20. Palawan Pr., Balabac I., Mangubat 519, iii-iv 06. INDONESIA. Bali: Kampoengan, Setchell BK4, 19 vi 29, Sanoer, Setchell BS137, 7 vi 29.

f. *submarina* Coll. and Herv.—PHILIP-

PINES. Luzon I.: Rizal Pr., Malabon, Quisumbing 262e, 16 x 31, Pasay Beach, McGregor 20 ii 15, Las Piñas, Quisumbing 6, 16 x 31. These may all be marine records. In the Berkeley herbarium there are several collections from freshwater localities in Batangas, Rizal, and Bataan provinces.

Enteromorpha lingulata J. Ag.

PHILIPPINES. Luzon I.: Rizal Pr., Pasay Beach, McGregor P44, v 14, Manila Bay, Merrill 4113, iv 05; Pangasinan Pr., Hundred Islands, Santos 1153, 9 v 38; Ilocos Norte Pr., Bonbon, Blanco 3067, 35. MARIANAS ISLANDS. Guam I., Nelson 500, 18, mouth of Pago R., Vatter 21, 25 i 46 (but cells rather large). MALAYA. Singapore, Holttum, 28-30. INDONESIA. Bali, Panganan, Setchell BP40, 46, 17 vi 29, Sanoer, Setchell BS136, 139, 7-15 vi 29.

Enteromorpha ramulosa (J.E. Smith) Hooker, *prox.*

PHILIPPINES. Luzon I.: Rizal Pr., Parañaque, Cruz 19550, viii 33; Ilocos Sur Pr., Magsingal, Collado, vi 20.

Enteromorpha spinescens (Kütz.) Kütz.

PHILIPPINES. Luzon I.: Ilocos Norte Pr., Paoay, Blanco 3074, ii 35.

Monostroma Thuret, 1854*Monostroma latissimum* (Kütz.) Wittr.

PHILIPPINES. Palawan Pr., Palawan I., Taytay, Merrill 9157, iv 13.

Ulva Linn., 1753*Ulva fasciata* Delile

INDIA. Travancore St., Trivandrum, Janaki and Erlanson, i 32, Cape Comorin, Janaki, 17 xii 32. INDONESIA. Sumatra: Belimbing, Kostermans 798, 20 x 38 (MICH). Java: Oedjoengkoelon, Kostermans 665, 18 x 38 (MICH), Pajoeng I., Kostermans 473, 14 x 38 (MICH), Parangtritis, Setchell JP451, Pameungpeuk, Setchell JP610, 613b, 617, 26 v 29, "South Coast," Teysman n.d. Bali: Panganan, Setchell BP79, 17 vi 29, Karang Asem, Pullai BK374, vi 33, Sanoer, Setchell BS150a, 198, 200, 15 vi 29.

Ulva lactuca L.

INDIA. Madras St., Krusadai I., Galaxie Reef, Janaki 924, 23 vi 32. PHILIPPINES. Luzon I.: Batanes Pr., Batan I., McGregor, vi 07; Cagayan Pr., Calayan I., McGregor, vi 07, Dalipuri I., Bartlett 15023, 31 x-5 xi 35 (MICH), Menabel, Edaño 78985, iv 30; Rizal Pr., Manila Bay, Ramirez 1, 5, 22 vi 35 (MICH); Ilocos Norte Pr., Bonbon, Blanco 3060, 35. INDONESIA. Moluccas: Ambon I., Robinson 575, 8 viii 13.

Ulva reticulata Forssk.

INDIA. Madras St., Krusadai I., Galaxie Reef, Janaki 26 vi 32 (MICH). PHILIPPINES. Luzon I.: Cagayan Pr., Menabel, Edaño, iv 30. Bohol Pr., Bohol I., Dimiao, McGregor, 4 vii 06. Cebu Pr., Bantayan I., McGregor, viii 06, Liloan, Bartlett 16204, 20 ii 35 (MICH). Mindanao I.: Zamboanga Pr., Pangapuyan I., Balhani 466, i-ii 41 (MICH), Lanhil I., Balhani 153, i-ii 41 (MICH). Basilan Pr., Sangboy I., Balhani 231, i-ii 41 (MICH), Saluping I., Balhani 871, i-ii 41 (MICH), Baluk-Baluk I., Balhani 731, 732, i-ii 41 (MICH). Sulu Pr., Tapul Group, Laminusa I., Abbott, 29 i 57 (BISH), Tawitawi I., Abbott, 12 ii 57 (BISH), Sitankai Reef, Yates 36275, x 19. MALAYA. Singapore, St. Johns I., Corner 23198, 31 xi 29. INDONESIA. Sumatra: Belimbing, Kostermans 780, 17 x 38 (MICH), "Sunda Strait" Teyman (MICH). Java: Taboehan, Kostermans 635, 17 x 38 (MICH). Bali: Sanoer, Setchell BS199, 15 vi 29, Kampoengan, Setchell BK22, 23, 19 vi 29.

CLADOPHORALES
CLADOPHORACEAE

Chaetomorpha Kützting, 1845*Chaetomorpha aerea* (Dillw.) Kütz.

INDONESIA. Java: Pameungpeuk, Setchell JP631j, 26 v 29.

Chaetomorpha antennina (Bory) Kütz.

INDONESIA. Sumatra: Benkuelen, v. Martens, 20 v 62. Java: Pameungpeuk, Setchell JP617, 618, 26 v 29, Parangtritis, Setchell JP454, 460, 461, v 29.

Chaetomorpha brachygona Harv.

PHILIPPINES. Luzon I.: Rizal Pr., Pasay Beach, McGregor, 28 ii 14 (in part).

Chaetomorpha crassa (C. Ag.) Kütz.

MALAYA. Singapore, Holttum 1928-30.

Chaetomorpha gracilis Kütz.

INDONESIA. Java: Tandjong Priok, Sandpoort, Setchell JT576, v 29.

Chaetomorpha indica Kütz.?

INDONESIA. Java: Pameungpeuk Reef, Setchell JP613g, 26 v 29. Filaments 70-100µ diam, cells 1.0-1.5, rarely 3 diam. long. Walls thin; cells not turgid (Børgesen, 1935:12).

Chaetomorpha linum (Müll.) Kütz.

PHILIPPINES. Batanes Pr., Batan I., McGregor 97, vi 07. Luzon I.: Cagayan Pr., Menabel, Edaño 78995B, 5 iv 30; Albay Pr., Albay Gulf, Curran 12264, vi 08; Rizal Pr., Montalban, Merrill 5096, iii 06; Ilocos Sur Pr., Magsingal, Collado, vi 20. INDONESIA. Java: Djakarta, Sakit I., Pullai JS594, 12 ix 29, Parangtritis, Setchell JP450, 462, 463, v 29. Bali: Patas, Pullai BP346, vi 33, Panganan, Setchell BP35, 17 vi 29, Sanoer, Setchell BS182, 7 vi 29.

Chaetomorpha spiralis Okam.

INDONESIA. Bali: Panganan, Setchell BP37, 17 vi 29. Specimens reported from the Philippines under the name of *C. torta* should probably be referred here (Okamura, 1936:68).

Chaetomorpha tortuosa (Dillw.) Kütz.

PHILIPPINES. Luzon I.: Cagayan Pr., Caminguin I., McGregor, Manila F.D., Manila, Merrill 7456, i-ii 11.

Rhizoclonium Kützting, 1843*Rhizoclonium crassipellitum* W. and G.S. West, v. *robustum* W. and G.S. West

PHILIPPINES. Luzon I.: Rizal Pr., Las Piñas, Rosario, 4 iii 32.

Rhizoclonium bookeri Kütz.

PHILIPPINES. Luzon I.: Bataan Pr., Lamao, Merrill 3516, x 03. INDONESIA. Java: Pangeran, Setchell JP534, v 29.

Cladophora Kützing, 1843*Cladophora aokii* Yamada

PHILIPPINES. Luzon I.: Bataan Pr., Limay, Shaw 1106, 24 iv 11. INDONESIA. Java: Pameungpeuk, Setchell JP597, 26 v 29. This, except for the heavy rhizoidal investment on the main axes, comes close to *C. prolifera* (Roth) Kütz.

Cladophora fascicularis (Mert.) Kütz.

INDIA. Madras St., Krusadai I., Janaki, 23 vi 32 (MICH). This may very well be the *C. monumentalis* Børgesen (1935:24), but the distinctions set up by him seem inadequate in view of the variability of the older species.

Cladophora quisumbingii n. sp.

Fig. 1

Plants tufted, 2–7 cm tall, not blackening when dried; basal cells distinct, without rhizoidal reinforcement; branching dense, the main axes not persisting, branches below opposite or 3–4-verticillate, or irregular, those above opposite, pseudodichotomous or alternate; cells near the base femur- to club-shaped with swollen ends, above becoming more cylindrical and in the ramelli cylindrical to slightly cask-shaped, the branchlet tips blunt and often a little enlarged; near the base the median cell diameter to 450 μ , the cells about 7 diameters long, in the middle portion of the plant 270–310 μ diam, the cells 4–5 diameters long, and in the ultimate ramelli 225–360 μ diam, the cells 1.5–7.0 diameters long; cell walls below very thick (to 70–90 μ) and often not collapsing when dried, but the walls in the ramelli about 7 μ thick. PHILIPPINES. Batanes Pr., Batan I., R.C. McGregor P45, vi 07 (UC-TYPE). Cagayan Pr., Cagayan Islands, Bawa, Edaña 78189, 3 xii 29.

Among the Philippine *Cladophoras* from Berkeley there were several mounts which seemed to be grouped under the name *C. prolifera* (Roth) Kütz., a rather improbable ascription considering the type locality of that species. Closer examination suggested the presence of at least two species: one, with rhizoids heavily covering the axes for three or even more degrees of branching from the base, which seemed to agree well with *C. aokii* Yam., while another of somewhat different habit lacked rhizoidal development altogether and was lighter in color, with heavy-walled lower cells.

From *C. aokii* the absence of rhizoids and coarser branches readily distinguish this second species. From *C. prolifera* the absence of rhizoids and lack of blackening, with details of habit, are sufficient. Some mounts bore the manuscript name of *C. quisumbingii*, which appears not to have been published, so it would seem appropriate to adopt it in recognition of the merits of the Philippine botanist, Dr. Eduardo Quisumbing.

Cladophora quisumbingii n. sp.

Fig. 1

Plantae fruticulosae, 2–7 cm altae, dum siccatae, nigrae non factae; cellulae basales perspicuae, sine rhizoideis; ramificatio densa, axibus principalibus non persistentibus, rami inferiores oppositi aut 3- aut 4-verticillati aut irregulares, superiores oppositi pseudodichotomi aut alterni; cellulae prope basim femoriformes ad clavatas, extremitatibus inflatis, supra magis cylindricae, in ramellis cylindricae ad paululum cupiformes, cacuminibus ramulorum obtusis et saepe aliquantum dilatatis; prope basim diametrus cellulae media ad 450 μ , cellulis ca. 7 plo longioribus quam latae, in partibus plantae mediis cellulae 270–310 μ diam, 4–5 plo longiores quam latae, in ramellis ultimis 225–360 μ diam, 1.5–7.0 plo longiores; membranae cellularum inferiorum crassissimae (ad 70–90 μ) dum siccatae saepe non collapse, membranae cellularum ramellorum, autem, ca. 7 μ crass. Plantae typicae in loco Batan I., Batan Pr., Rep. Philippinensis dicto, ab R.C. McGregor P45, m. Jun. 1907 lectae, in herb. Univ. Californiensis (Berkeley) depositae.

Cladophora sibogae Reinb.

INDONESIA. Java: Pangendaran, Setchell JP535, 536, v 29. Axes to 165 μ , branchlets to 60 μ diam.

Cladophora socialis Kütz.

INDONESIA. Java: Pangendaran, Setchell (det.) JP533, v 29. Axes to 80 μ , branchlets to 45 μ diam, and flagellar branchlets frequent.

SIPHONOCLOADIALES
DASYCLADACEAE*Dasycladus* C. Agardh, 1827*Dasycladus australicus* (Sond.) Cram.

PHILIPPINES. Catanduanes Pr., Catanduanes I., Calolbon, Ramos and Edaña 77262. Sporangia 360–400 μ diam, spores 66–73 μ diam, sporangia solitary-terminal on the first ramular segment. The 4 secondary segments are quickly dropped.

Halicoryne Harvey, 1859

Halicoryne wrightii Harv.

PHILIPPINES. Luzon I.: Pangasinan Pr., Hundred Islands, Santos 1154, 9 v 38. INDONESIA. Bali: Boeleleng, Setchell BB103, 19 v 29, Karang Asem, Pullai BK358, vi 33, Kampo-

engan, Setchell BK646, vi 29, Patas, Pullai BP344, vi 33.

Neomeris Lamouroux, 1816

Neomeris annulata Dickie

INDONESIA. Bali: Kampoengan, Setchell BK650c, vi 29.

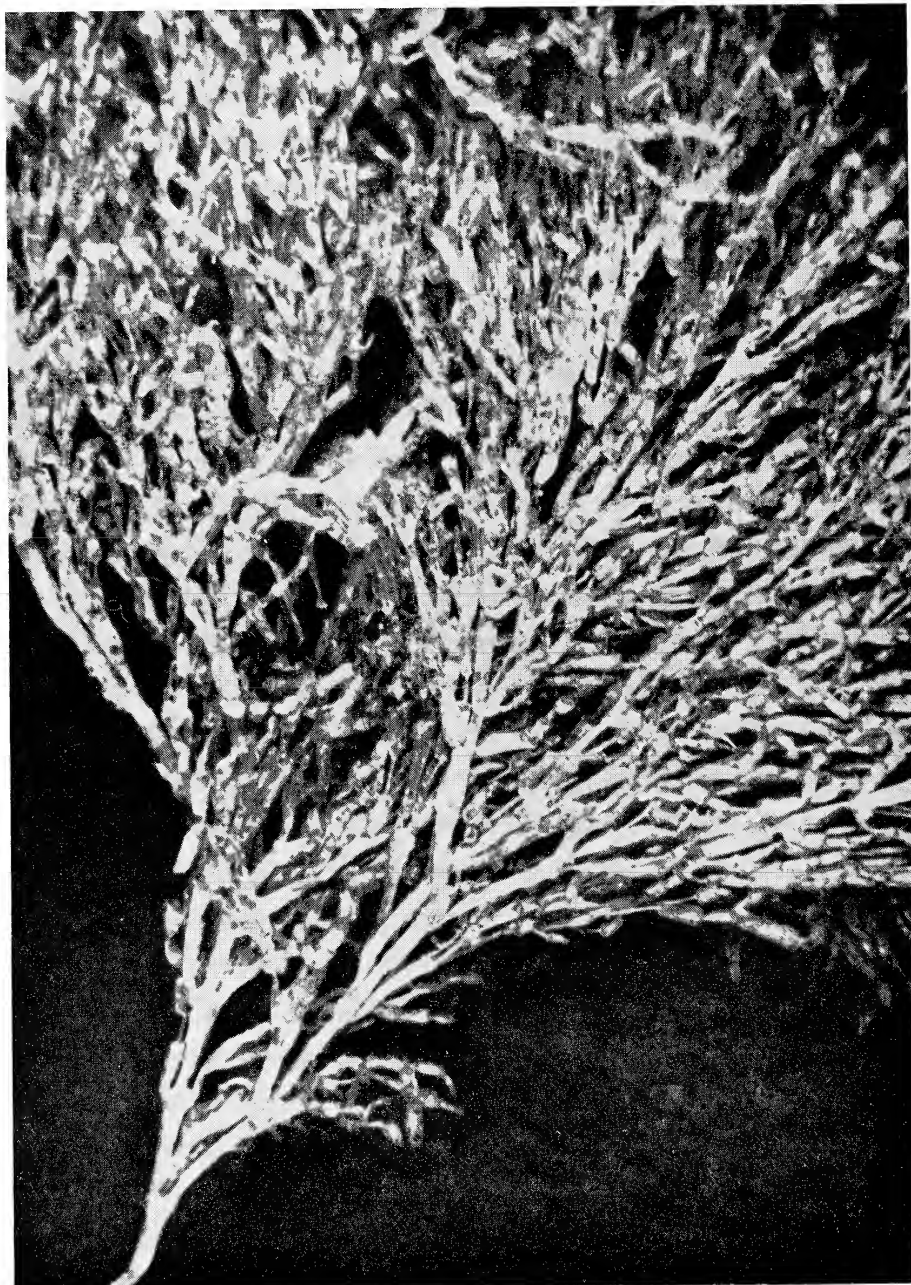


FIG. 1. *Cladophora quisingii*, a small plant showing the coarse branching, $\times 65$.

Neomeris dumetosa Lamour.

INDONESIA. Java: Djakarta Bay, Amsterdam I., Kostermans 410, 11 x 38 (MICH).

Neomeris vanbosseae Howe

PHILIPPINES. Palawan Pr., Balabac I., Abbott, 1 iii 57 (BISH). MALAYA. Singapore, Punggol, Holttum, 6 viii 28. INDONESIA. Java: Thousand Islands, Kaliage I., Kostermans 174, 5 x 38 (MICH), Tjina I., Kostermans 342, 6 x 38 (MICH), Pangendaran, Setchell 550B, 550C, v 29. Bali: Boeleleng, Setchell BB103B, 20 vi 29.

Bornetella Munier-Chalmas, 1877

Bornetella capitata (Harv.) J. Ag.

INDONESIA. Java: Thousand Islands, Amsterdam I., Kostermans 415, 11 x 38 (MICH), Kaliage I., Kostermans 197 p.p., 5 x 38 (MICH), Kelapa I., Kostermans 276, 5 x 38 (MICH), Ijina I., Kostermans 346, 6 x 38 (MICH).

Bornetella nitida (Harv.) Munier-Chalmas

PHILIPPINES. Mindoro I.: Mindoro Oriental Pr., Puerto Galera, Medina 571, 23 iv 29. INDONESIA. Bali: Boeleleng, Setchell BB97, 19 vi 29, Kampoengan, Setchell BK3, 16 vi 29. Celebes: Macassar, Setchell M502, 503, 22–23 vi 29.

Bornetella oligospora Solms-Laub.

INDONESIA. Java: Thousand Islands, Kaliage I., Kostermans 173, 5 x 38 (MICH), Ijina I., Kostermans 341, 6 x 38 (MICH), Kelapa I., Kostermans 274, 5 x 38 (MICH).

Bornetella sphaerica (Zanard.) Solms-Laub.

PHILIPPINES. Mindoro I.: Mindoro Oriental Pr., Puerto Galera, Medina 556, n.d. Bohol Pr., Bohol I., McGregor 64, vii 06. INDONESIA. Java: Kaliage I., Kostermans 197, 5 x 38 (MICH).

Acetabularia Lamouroux, 1816

Acetabularia philippinensis Gilbert

PHILIPPINES. Luzon I.: Pangasinan Pr., Anda I., Clemens 6884, 31 iii 25. Palawan Pr., Palawan I., Puerto Princessa, McGregor, x 25.

VALONIACEAE

Valonia Ginnani, 1757

Valonia aegagropila C. Ag.

PHILIPPINES. Basilan Pr., Sibakel I., Balhani, i–ii 41 (MICH). INDONESIA. Java: Djakarta Bay,

Leiden I., Kostermans 74, 28 ix 38 (MICH). Bali: Panganan, Setchell BP44, 652c, 17 vi 29. Sanoer, Setchell BS135, 141, 15 vi 29.

Valonia fastigiata Harv.

PHILIPPINES. Mindanao I.: Zamboanga Pr., Pangapuyon I., Balhani 174a, i–ii 41 (MICH), Cabulay I., Balhani 286, i–ii 41 (MICH). Sulu Pr., Sibutu I., Abbott, 19 ii 57 (MICH). INDONESIA. Sumatra: Lampoeng Bay, Seboekoe, Kostermans 722, 19 x 38 (MICH). Celebes I.: Macassar, Weber-van Bosse 929, xi 88 (MICH).

Valonia ventricosa J. Ag.

PHILIPPINES. Cebu Pr., Cebu I., Minglanilla, McGregor, 16 x 06. Sulu Pr., Sibutu I., Abbott, 19 ii 57 (BISH). INDONESIA. Java: Thousand Islands, Ijina I., Kostermans 345, 6 x 38 (MICH).

Boergesenia Feldmann, 1938

Boergesenia forbesii (Harv.) Feldm.

PHILIPPINES. Luzon I.: Cagayan Pr., Calayan I., McGregor, vi 07; Ilocos Norte Pr., Currimao, Bartlett 14972, 14973, 28 x 35 (MICH). INDONESIA. Sumatra: Belimbing, Kostermans 757, 20 x 38 (MICH). Java: Oedjoengkoelon, Kostermans 662, 18 x 38 (MICH), Djakarta Bay, Amsterdam I., Kostermans 414, 11 x 38 (MICH), Leiden I., Kostermans 75, 28 ix 38 (MICH), Ijina I., Kostermans 344, 6 x 38 (MICH), Pangendaran, Setchell JP630, v 29.

Valoniopsis Børgesen, 1934

Valoniopsis pachynema (Mart.) Børg.

PHILIPPINES. Luzon I.: Cagayan Pr., Babuyan Islands, Dalupiri I., Bartlett 15027, 35 (MICH); La Union Pr., San Fernando, Fénix 13007, xii 10. These were confirmed earlier (Taylor, 1961), but in general Philippine records were at that time referred to *Cladophoropsis philippinensis*. INDONESIA. Sumatra: Benkuelen, *ex herb.* v. Martens and probably an isotype specimen. Java: Oedjoengkoelon, Kostermans 661, 18 x 38 (MICH). Taboehan, Kostermans 663, 17 x 38 (MICH), Parangtritis, Setchell JP464, v 29, Pangendaran, a particularly fine mount, Setchell JP531, v 29, Pameungpeuk, Setchell JP596, 619b, 26 v 29. Bali: Karang Asem,

Pullai BK367, vi 33, Sanoer, Setchell BS140, 7 vi 29, Panganan, Setchell BP14-43, 46a, 17 vi 29.

Dictyosphaeria Decaisne, 1842

Dictyosphaeria cavernosa (Forssk.) Børg.

PHILIPPINES. Luzon I.: Batangas Pr., Batangas Channel, Bartlett 14615, 35 (MICH). Palawan Pr., Palawan I., Taytay, Merrill 9045, iv 13, Puerto Princesa, Santos 703, 8 iv 37 (MICH). Sulu Pr., Tawitawi I., Abbott, 12 ii 57 (BISH), Tijitiji Reef, Abbott, 15 ii 57 (BISH), Sibutu I., Abbott, 17 ii 57 (BISH), Sitankai Reef, Abbott, 17 ii 57 (BISH), Turtle Islands Balabac I., Abbott, 2 iii 57 (BISH). MALAYA. Singapore, Binder n.d., St. Johns I., Corner 23677, 31 xii 29. INDONESIA. Java: Djakarta Bay, Amsterdam I., Kostermans 418, 11 x 38 (MICH), Kelapa I., Kostermans 298, 5 x 38 (MICH).

Dictyosphaeria intermedia Weber-van Bosse

PHILIPPINES. Luzon I.: Cagayan Pr., Bawa, Edaño 78192, xii 29, Menabel, Edaño 78994, n.d. MARSHALL ISLANDS. Kwajalein Atoll, Loj-jairok I., Fosberg 3412, 15 i 52 (MICH).

Dictyosphaeria setchellii Børg.

INDONESIA. Java: Oedjoengkoelon, Kostermans 663, 18 x 38 (MICH), Toenda I., Kostermans 574, 15 x 38 (MICH), Djakarta Bay, Amsterdam I., Kostermans 418, 11 x 38 (MICH).

Dictyosphaeria versluisii Weber-van Bosse

INDONESIA. Bali: Oie Yong Seng B322, 1929-1930, Sanoer, Setchell BS214, 250, 7-15 vi 29.

Cladophoropsis Børgesen, 1905

Cladophoropsis membranacea (Forssk.) Børg.

MARIANAS ISLANDS. Guam I., Radin, viii 45, Vatter 20, 25 i 46 (with rather slender filaments). INDONESIA. Bali: Sanoer, Setchell BS6536, 15 vi 29 (filaments to 135 μ diam).

Cladophoropsis philippinensis Taylor

(For numerous stations see Taylor, 1961). PHILIPPINES. Mindanao I.: Zamboanga Pr., Manicaan, Balhani 383, Logoy, 438, Bolong, 273, 506, Taluksangay, 404, Pangapuyon I.,

173, Buena Vista, 482, Panubigan I., 496, all Balhani i-ii 41 (MICH). Basilan Pr., Basilan I., Lamitan 322, Kilay I., 697, Tundun Pasil, 377, Panigayan Islands, 628, all Balhani i-ii 41 (MICH). It is curious that this species, so far, appears endemic to the area about Basilan I. and neighboring Zamboanga.

Cladophoropsis sundanensis Reinb.

INDONESIA. Java: Oedjoengkoelon, Kostermans 657, 18 x 38 (MICH), Djakarta Bay, Leiden I., Kostermans 77, 28 ix 38 (MICH), Parangtritis, Setchell JP466, v 29.

Spongocladia Areschoug, 1853

Spongocladia vaucheriaeformis Aresch.

PHILIPPINES. Sulu Pr., Tawitawi Group, Tawitawi I., Abbott, 13 ii 57 (BISH). MALAYA. Singapore, ii 83 (*ex herb.* Hauck, MICH). INDONESIA. Java: Thousand Islands, Amsterdam I., Kostermans 409, 11 x 38 (MICH), Hoorn I., Setchell JH581, 1 v 29, Kelapa I., Kostermans 277, 5 x 38 (MICH). These are large plants, exceeding 15 cm in height, freely if irregularly branched, the dried divisions 5-8 mm diam. The habit is similar to some of the bushy codiums, or sometimes the terminal divisions are rather crowded and erect. Comparison was made with Mauritius specimens from Areschoug's herbarium in the Rijksmuseum, Stockholm.

Spongocladia dichotoma Zanard.

PHILIPPINES. Luzon I., Pangasinan Pr., Alominos, Fénix, x 28 (? in part) (UC). NEW GUINEA: Tami, 75, 1894 (NY). Some plants in the Fénix collection were very loosely and irregularly branched, and suggest *S. dichotoma*; others had the habit of *S. vaucheriaeformis*, but these may not be different species after all. Comparison was made with Sorong, New Guinea material *leg.* Beccari in the British Museum N.H. herbarium, for which Zanardini originally intended the name *Spongodendron dichotomum*. In the Tami material the filament diameter ranged from 55 to 330 μ , in that from Sorong 80-200 μ .

Spongocladia neocaledonica Grunow

INDONESIA. Bali: Oie Yong Seng, B322a, 29-30; Panganan, Setchell BP71, 17 vi 29; Sanoer, Setchell BS251, 15 vi 29 (all UC). Com-

parison was made with Poro, New Caledonia material *leg.* Grunow in the British Museum N.H., and in Grunow's herbarium in the Naturhistorisches Museum, Vienna. All had the same cushion form, often with short prominences 0.5–1.0 cm high on the upper side. The degree of compactness varied considerably. The filaments were commonly clavate at the tips, often irregularly so and lobed, leading to irregular branching, although the basic branching was dichotomous. Whereas the filaments in the general mass were 100–200 μ diam, in these tips they commonly ranged from 150 to 400 μ and, if lobed for forking, to 625 μ . Cross-walls were very irregularly placed and were seldom seen near the tips, often not for distances as much as 1 cm from the tips, so that branching and rebranching might occur several times before a cross-wall intervened.

The writer is reluctant to follow Papenfuss' (1950) relegation of these plants to *Cladophoropsis*, not having had field experience with them. So far as he can see, the branch tips of the erect forms, where the plant shape is established, are relatively free from associated sponge tissue, and the plant form does not seem to vary with the degree of sponge investment. Association of other green and red algae with sponges is often met in the tropics, and no special plant form appears to result—notably, indeed, in the case of *Cladophoropsis* itself, in Caribbean waters.

Boodlea Murray & DeToni, 1890

This genus always seems difficult, the species ill-defined. While other genera, such as *Microdictyon*, sometimes show boodleoid proliferations, it is not these which cause the trouble, but rather tussocks which seem generically characteristic but specifically intermediate.

Boodlea composita (Harv.) Brand

INDONESIA. Java: Oedjoengkoelon, Kostermans 658, 18 x 38 (MICH), Toenda I., Kostermans 578, 15 x 38 (MICH), Kaliage I., Kostermans 198, 5 x 38 (MICH), Pameungpeuk, Setchell JP613f, 15 vi 29.

Boodlea paradoxa Reinb.

INDONESIA. Bali: Kampoengan, Setchell BK463 (*prox.*), vi 29.

Microdictyon Decaisne, 1839

Microdictyon montagnei Harv.

PHILIPPINES. Mindanao I.: Zamboanga Pr., San Ramon, Copeland, n.d. Sulu Pr., Siasi I., Abbott, 28 i 57 (BISH), Sitankai Reef, Yates 36277, x 19, Tawitawi I., Abbott, 12 ii 57 (BISH). MALAYA. Singapore, St. Johns I., Nur, ix 27. INDONESIA. Bali: Sanoer, Den Pasao, Setchell BS177, 7 vii 29, Sanoer Reef, Setchell BS185, 236, 15–18 vii 29, Panganan, Setchell BP69, 70, 17 vi 29. Plants of this species (and in fact, though to a lesser degree, many members of the genus) proliferate very considerably out of the initial plane, sometimes appearing with plane blades, sometimes simulating minute *Boodlea* plants.

Anadyomene Lamouroux, 1812

Anadyomene brownii (Gray) J. Ag.

PHILIPPINES. Palawan Pr., Balabac I., Abbott, 1 iii 57 (BISH); Sulu Pr., Turtle Islands, Taganak I., Abbott, 23 ii 57 (BISH). INDONESIA. Bali: Boeléleng, Setchell BB108 20 vi 29. Frequency of septa is a very variable character in this species, which *A. esepata* Gilbert much resembles.

Anadyomene plicata C. Ag.

PHILIPPINES. Mindoro I.: Mindoro Occidental Pr., Lubang, Villaflores 35, 11–17 ix 35 (MICH). INDONESIA. Java: Oedjoengkoelon, Kostermans 669, 18 x 35 (MICH), Pajoeng I., Kostermans 462, 14 x 38 (MICH), Ijina I., Kostermans 374, 6 x 38 (MICH), Pameungpeuk Reef, Setchell JP597, 26 v 29, Kelapa I., Kostermans 270, 5 x 38 (MICH). Bali: Kampeongan, Setchell BK641, 649c, vi 29, Panganan, Setchell BP83d, 17 vi 29.

SIPHONALES

BRYOPSIDACEAE

Bryopsis Lamouroux, 1809

Bryopsis plumosa (Huds.) C. Ag., *prox.*

MALAYSIA. Singapore, St. Johns I., Corner 23197, 31 xii 29. While the specimens in this collection agree quite well with this species in a coarse form, having the branchlets to 265 μ diam, others from the Singapore area showed

repeated divisions of the main axes, with very numerous penultimate divisions but few ramelli upon them, producing a quite different habit. In the herbarium of the University of California they have been referred to *B. harveyana* J. Ag., but that name is based on *B. plumosa* v. *secunda* Harv. (*B. pennata* v. *secunda* [Harv.] Coll. & Herv.), a West Indian plant not identical in character.

CAULERPACEAE

Caulerpa Lamouroux, 1809

Caulerpa brachypus Harv.

PHILIPPINES. Sulu Pr., Sibutu I., Abbott, 19 ii 57 (BISH). INDONESIA. Bali: Sanoer, Setchell BS131, 7 vi 29.

Caulerpa cupressoides (West) C. Ag., v. *cupressoides*

MARIANAS ISLANDS. Saipan I., Tanapag Harbor, Kruckeberg, 15 vi 45 (MICH). INDONESIA. Java: Pameungpeuk Reef, Setchell JP605, 25 v 29.

v. *disticha* Weber-van Bosse—INDIA. Madras St., Krusadai I., Pamban, Janaki 933, 24 vi 32 (MICH).

v. *lycopodium* (J. Ag.) Weber-van Bosse—MARIANAS ISLANDS. Guam I., Thompson 460, ca. 1912.

v. *mamillosa* (Mont.) Weber-van Bosse—LINE ISLANDS. Christmas I., London, Fosberg and Metraux 13240, 26 viii 30 (MICH).

Caulerpa lentillifera J. Ag., v. *lentillifera*

PHILIPPINES. Luzon I.: Camarines Norte Pr., Malbulao, Vivas and Roma, 21 i 35. Palawan Pr., Palawan I., Puerto Princessa, McGregor P36, x 25. Mindanao I.: Misamis Occidental Pr., Baliangao, Cabugan I., Manacop 5135, iv 36. Sulu Pr., Turtle Islands, Taganak I., Abbott, 23 ii 57 (BISH).

v. *longistipitata* Weber-van Bosse—MALAYA. Singapore, Holttum, 1928–30. PHILIPPINES. Sulu Pr., Sibutu I., Abbott, 19 ii 57. The stalks are much longer than the distal diameter of the ramelli, but these are not distichous in arrangement.

Caulerpa mexicana (Sond.) J. Ag.

INDIA. Madras St., Krusadai I., Pamban, Janaki 934, 24 vi 32 (MICH). MALAYA. Singa-

pore, Blakang Mati I., Corner 23190, ii 30. PHILIPPINES. Palawan Pr., Palawan I., Taytay, Merrill 9143, iii 13. Balabac I., Calandorang Bay, Abbott 1 iii 57 (BISH). HAWAII. Laysan I., Tanager Exped. 56, 60b, 1923 (MICH). This species appeared in earlier publications on Philippine algae under the name *C. crassifolia* (C. Ag.) J. Ag.

Caulerpa microphysa (Weber-van Bosse) Feldm.

MAURITIUS. Ilôt Barkly, G. Morin 813 (isotype of *C. lentillifera* f. *parvula* Børg.), 24 iv 48, 861, 10 v 48, 1174, 30 x 51 (all WRT). Cfr Børgesen 1949, p. 18. PHILIPPINES. Basilan Pr., Basilan I., Boboh, Balhani 754, i–ii 41 (MICH), Atong Atong, Balhani 62, i–ii 41 (MICH), Lukapsi, Balhani 616, i–ii 41 (MICH), Mindanao I.: Zamboanga Pr., Labuan, Balhani 428, i–ii 41 (MICH), Manicahan, Balhani 389, i–ii 41 (MICH), Sakol I., Balhani 428, i–ii 41 (MICH). INDONESIA. Java: Toenda I., Koster-mans 589, 15 x 38 (MICH), Pajoeng I., Koster-mans 468, 14 x 38 (MICH).

Caulerpa peltata Lamour., v. *peltata*

INDIA. Madras St. Krusadai I., Pamban, Janaki 927, 24 vi 32. PHILIPPINES. Luzon I.: Pangasinan Pr., Lingayen Gulf, Santos 1151, 9 v 38; Ilocos Sur Pr., Magsingal, Collado, n.d. MALAYA. Singapore, Holttum, 1928–30. INDONESIA. Java: Djakarta, Sakit I., Pullai JS593, ix 29. Bali: Boeleleng, Setchell BB99, 20 vi 29, Panganan, Setchell BP30, 17 vi 29.

v. *macrodisca* (Dec.) Weber-van Bosse—MALAYA. Singapore, Holttum 1928–30. Disks ranged to 20 mm diam when soaked (16 mm when dry). Gilbert's paper (1942) reports them even larger from Panay.

Caulerpa racemosa (Forssk.) J. Ag. (specimens typical or not varietally distinctive)

INDIA. Madras St., Visakhapatnam, T. Sreeramulu, 1961 (WRT). PHILIPPINES. Luzon I.: Cagayan Pr., Claveria, Velasco 3011, n.d.; Ilocos Sur Pr., Magsingal, Collado, vi 20; Ilocos Norte Pr., Bonbon, Blanco, 1936. Panay I.: Antique Pr., Semirara I., Alcasid 6923, iii 40. Palawan Pr., Balabac I., Abbott, 1 iii 57 (BISH). Sulu Pr., Tawitawi Group Tawitawi I., Tjijitiji Reef, Abbott, 15 ii 57 (BISH); Sibutu I., Tun-

undao Reef, Abbott, 17 ii 57 (BISH); Cagayan Sulu I., Jurata Bay, Abbott, 23 ii 57 (BISH), Turtle Islands, Taganak I., Abbott, 23 ii 57 (BISH). INDONESIA. Bali: Sanoer, Setchell *BS128-130*, 132, 133, 6-15 vi 29, Panganan, Setchell *BP652B*, vi 29. Celebes: Macassar, Weber-van Bosse, 1888. MARIANAS ISLANDS. Saipan I., Tanapag Harbor, Kruckeberg, 3 vii 45 (MICH). Guam I., Thompson 427, v 12, Pago R., Vatter 16, 25 i ? HAWAII. Laysan I., Tanager Exped. 28, n.d. (MICH).

v. *chemnitzia* (Esper) Weber-van Bosse—INDIA. Madras St., Trivandrum, Janaki and Erlanson, i 34 (MICH), Krusadai I., Pamban, Janaki 928, 932, 940, 946, 26 vi 32 (MICH).

v. *clavifera* (Turn.) Weber-van Bosse—PHILIPPINES. Luzon I.: Pangasinan Pr., Alaminos, McGregor xii 22, Dagupam, Bureau of Forestry 3128, vi 34. Mindanao I.: Zamboanga Pr., Sibago I., Balhani 125, i-ii 41; Misamis Occidental Pr., Baliangao, Manacop 5126, iii 36 (MICH). Basilan Pr., Basilan I., Lamitan, Balhani 528, i-ii 41 (MICH). MARIANAS ISLANDS. Guam I., Thompson 1912. MALAYA. Singapore, Tanjong Panggol, Holttum, 27 xi 27. INDONESIA. Celebes, Macassar, Weber-van Bosse 1888.

v. *cornephora* (Mont.) Weber-van Bosse—INDIA. Madras St., Krusadai I., Janaki 928, 931, 23, 24 vi 32.

v. *laetevirens* (Mont.) Weber-van Bosse—PHILIPPINES. Cebu Pr., Bantayan I., Manacop 5141, v 36. Mindanao I.: Zamboanga Pr., Pangapuyon I., Balhani 179, i-ii 41 (MICH). Sulu Pr., Sibutu I., Abbott, 19 ii 57 (BISH), Sitankai Reef, Yates, n.d. MARIANAS ISLANDS. Guam I., Thompson 428, 1912. HAWAII. Laysan I., Tanager Exped., 1923 (MICH). Necker I., Christophersen, vii 24 (MICH).

v. *lamourouxii* (Turn.) Weber-van Bosse—TONGA ISLANDS. Tonga Tapu, McKern 29, ix 20-vi 21 (MICH).

v. *macrophysa* (Kütz.) Taylor—The several specimens reported by Gilbert (1942, 1961) under this name hardly reach the size to be expected, and come close to v. *occidentalis*. Even in those reported here, which agree more closely in this respect, the ramelli are rather small and hardly as depressed on the end as in the Florida form (Taylor, 1928, 1960). However, this character does not seem to have been

a criterion applied by Kützing in distinguishing the variety. PHILIPPINES. Cebu Pr., Bantayan I., Manacop 5144, v 36. INDONESIA. Bali: Panganan, Setchell *BP31*, 17 vi 29.

v. *occidentalis* (C. Ag.) Børg.—PHILIPPINES. Luzon I.: Rizal Pr., Manila Bay, Quisumbing 82258, 16 v 29. Mindanao I.: Zamboanga Pr., Little Santa Cruz I., Bartlett 16144, 19 ix 35 (MICH). Sulu Pr., Tapul Group, Laminusa I., Abbott, 30 i 57 (BISH).

Caulerpa serrulata (Forssk.) J. Ag.

PHILIPPINES. Luzon I.: Pangasinan Pr., Hundred Islands, Santos 1149, 9 v 38; Ilocos Sur Pr., Cabugao, Blanco 3075, Magsingal, Collado 10, vi 20. Mindoro I.: Mindoro Oriental, Puerto Galera, Santos 565, 31 xii 36. Palawan Pr., Balabac I., Abbott, 2 iii 57 (BISH). INDONESIA. Bali: Boeileleng, Setchell *BB98a*, vi 29, Kampungan, Setchell *BK645a*, 646, 650a, e, vi 29. MARSHALL ISLANDS. Ujae Atoll, Bock I., 34348a; Lae Atoll, Enament I., 34086, Pokak Atoll, Sibylla I., 34514; Bikar Atoll, Bikar I., 34561; Utirik Atoll, Eluk I., 33706a; Ailuk Atoll, Ailut I., 33954, all Fosberg 1951-52 (MICH). LINE ISLANDS. Palmyra I., Vasconcellos 2951, vii 40.

Caulerpa sertularioides (Gmel.) Howe (specimens typical or not varietally distinctive)

PHILIPPINES. Mindoro I.: Mindoro Oriental Pr., Puerto Galera, Santos 573, 31 xii 36, Velasquez 747, 31 iii 41 (MICH), Balatera Malaki, Velasquez 7689, iv 41 (MICH). MARIANAS ISLANDS. Guam I., between Ylig and Togcha Bays, Moore 401, 7 iv 46 (MICH). CAROLINE ISLANDS. Truk Group, Moen I., Stone 2181, viii 57 (MICH). INDONESIA. Java: Djakarta, Sakit I., Pullai *JS592*, 12 ix 29, Kampungan, Setchell *BK643*, vi 29.

v. *sertularioides* f. *brevipes* (J. Ag.) Sved.—INDIA. Madras St., Krusadai I., Pamban, Janaki 24 vi 32 (MICH). PHILIPPINES. Luzon I.: Rizal Pr., Manila Bay, Quisumbing 5204, 12 ix 28. Sulu Pr., Pearl Bank, Kienholz, vi 23, Turtle Islands, Taganak I., Abbott, 23 ii 57 (BISH). INDONESIA. Bali, Boeileleng, Pullai *BB387*, vii 33.

v. *sertularioides* f. *longiseta* (Bory) Sved.—PHILIPPINES. Luzon I.: Rizal Pr., Manila Bay, Guitierrez 85755, viii 33; Ilocos Sur Pr., Mag-

singal, Collado, vi 20; Ilocos Norte Pr., Currimao, Collado, vi 20. Palawan Pr., Palawan I., Puerto Princesa, Santos 646, 3 iv 37 (MICH). Mindanao I.: Zamboanga Pr., Little Santa Cruz I., Bartlett 4203, i-ii 41 (MICH), Lanhil I., Bartlett 162, i-ii 41 (MICH). Basilan Pr., Saluping I., Balhani 874, i-ii 41 (MICH), Malamaui, Balhani 64, i-ii 41 (MICH). MALAYA. Singapore, Tandjung Punggol, Holttum, 27 xi 27. INDONESIA. Java: Tjina I., Kostermans 324, 6 x 38 (MICH).

Caulerpa taxifolia (Vahl) C. Ag.

INDIA. Madras St., Krusadai I., Pamban, Janaki 936, 24 vi 32 (MICH). MALAYA. Singapore, Holttum, 1928-30. INDONESIA. Java: Anger, Kostermans 611a, 16 x 38 (MICH); Pajoeng I., Kostermans 467c, 14 x 38 (MICH); Djakarta, Setchell JB567, v 29.

Caulerpa urvilliana Mont.

PHILIPPINES. Palawan Pr., Palawan I., Puerto Princesa, McGregor, x 25. Sulu Pr., Pearl Bank, Kienholz, vi 23; Sibutu I., Abbott, 19 ii 57 (BISH). MARSHALL ISLANDS. Ujelang Atoll, Ujelang I., 34191; Wotho Atoll, Wotho I., 3417, Eneobank I., 34437; Ujae Atoll, Bock I., 34348b; Bikar Atoll, Jaliklik I., 34583; Utirik Atoll, Eluk I., 33706b; Likiep Atoll, Lado I., 33795, all Fosberg 1951-52 (MICH); Arno Atoll, Pikarej I., Anderson 3755, 23 v 50.

Caulerpa vesiculifera (Harv.) Harv.

PHILIPPINES. Palawan Pr., Palawan I., Puerto Princesa, McGregor, x 25.

CODIACEAE

Chlorodesmis Harvey & Bailey, 1851

Chlorodesmis comosa Harv. and Bail.

PHILIPPINES. Luzon I.: Pangasinan Pr., Alaminos, Fénix, x 28.

Chlorodesmis hildebrandtii A. and E.S. Gepp

PHILIPPINES. Sulu Pr.; Sibutu I., Abbott, 19 ii 57 (BISH). MARIANAS ISLANDS. Saipan I., Tanapag Harbor, Kruckeberg, 3 vii 45 (MICH).

Chlorodesmis torresiensis Taylor

PHILIPPINES. Luzon I.: Cagayan Pr., Menabel, Edaño 79001, 78995A, iv 30. Filament diame-

ters to 350 μ . Segments transverse-ended, with the constrictions equally placed.

Avrainvillea Decaisne, 1842

Avrainvillea erecta (Berk.) A. and E.S. Gepp

PHILIPPINES. Palawan Pr., Balabac I., Abbott, 2 iii 57 (BISH). MALAYA. Singapore, Holttum, 1928-30, Tanjong Ponggol, Holttum, 27 xi 27.

Avrainvillea lacerata J. Ag.

PHILIPPINES. Luzon I.: Pangasinan Pr., Alaminos, Fénix 13, 7 x 28. INDONESIA. Java: Pangendaran, Setchell JP547, 549c, v 29.

Avrainvillea obscura J. Ag.

MARIANAS ISLANDS. Saipan I., Tanapag Harbor, Kruckeberg, 5 vii 45 (MICH). The habit of these plants agrees excellently with this species, better than with *A. erecta*, but the surface filaments show a little brown discoloration.

Cladocephalus Howe, 1905

Cladocephalus sp.

PHILIPPINES. Palawan Pr., Balabac I., Gnat Reef, Abbott, 4 iii 57 (BISH). These specimens were in the form of a small tuft, with several short, stout, erect stems terminating in groups of rounded, slightly zonate blades 1-2 cm broad. The central blade filaments reached 15.5 μ diam. Those at the surface were 5.5-7.8 μ diam, less densely entangled than those of the West Indian *C. luteofuscus* (Crouan) Børg. This is a most interesting thing to find in the area, but one hesitates to describe it as new on so little material, and material which is possibly dwarfed.

Tydemania Weber-van Bosse, 1911

Tydemania expeditionis Weber-van Bosse

PHILIPPINES. Sulu Pr., Tawitawi I., Abbott, 12 ii 57 (BISH). INDONESIA. Java: Thousand Islands, Kostermans 177, 5 x 38 (MICH).

Udotea Lamouroux, 1812

Udotea argentea Zanard., v. *spumosa* A. and E. S. Gepp.

PHILIPPINES. Palawan Pr., Palawan I., Taytay,

Merrill 9140, iv 13; Balabac I., Abbott, 2 iii 57 (BISH). Sulu Pr., Turtle Islands, Taganak I., Abbott, 24 ii, 23 iii 57 (BISH).

Udotea flabellum (E. and S.) Howe

MALAYA. Singapore, Binder (*ex herb.* Trinity Coll., Dublin).

Udotea glaucescens Harv.

MALAYA. Singapore, Dodol I., Burkill 3007 (WRT).

Udotea javensis A. and E.S. Gepp

INDONESIA. Java: Thousand Islands, Amsterdam I., Kostermans 416, 11 x 38 (MICH), Kaliage I., Kostermans 201, 5 x 38 (MICH), Kerkhof I., Kostermans 7, 26 ix 38 (MICH).

Udotea orientalis A. and E.S. Gepp

PHILIPPINES. Cagayan Pr., Babuyan Islands, Calayan I., McGregor, *p.p.*, 1903. Palawan Pr., Balabac I., Abbott, 2 iii 57 (BISH). Sulu Pr., Turtle Islands, Taganak I., Abbott 24 ii 57 (BISH). INDONESIA. Bali: Boecleng, Pullai BB395, viii 33, Kampoengan, Setchell BK2, 642, 643, 16 vi 29.

Halimeda Lamouroux, 1812

This genus has recently been reviewed by L. W. Hillis (1959), who included most of the Pacific material available at that time in her report. Her listings, therefore, should be considered together with the specimens cited here in reaching a conception of the *Halimeda* flora of the Indian and Pacific Oceans.

Halimeda bikinensis Taylor

INDONESIA. Bali: Karang Asem, Pullai BK-376, vi 33.

Halimeda cylindrica Dec.

PHILIPPINES. Luzon I.: Quezon Pr., Tayabas Bay (?), Yates 25831, xii 16. Palawan Pr., Culion I., Culion, Bartlett 15578, 27 vii 35 (MICH).

Halimeda discoidea Decaisne v. *discoidea*

PHILIPPINES. Palawan Pr., Palawan I., Taytay, Merrill 9147, vi 13, Balabac I., Pasig Bay, Abbott, 1 iii 57 (BISH). Sulu Pr., Tapul Group, Laminusa I., Abbott, 29 i 57 (BISH), Pearl

Bank, Kienholz, vi 23, Cagayan Sulu, Abbott, 4 iii 57 (BISH). INDONESIA. Bali: Sanoer, Setchell BS145, 15 vi 29.

v. *discoidea* f. *subdigitata* Gilbert—PHILIPPINES. Palawan Pr., Balabac I., Abbott, 4 iii 57 (BISH). Sulu Pr., Sibutu I., Abbott, 19 iii 57 (BISH).

Halimeda gracilis Harv.

MALAYA. Singapore, Holtum, 1928–30.

Halimeda macroloba Decaisne

PHILIPPINES. Luzon I.: Quezon Pr., Alabat I., Santos 794, 20 x 37; Camarines Norte Pr., Basiad, Yates 25829, xii 16; Pangasinan Pr., Hundred Ids., Santos 1150, 9 v 38, Alominos, Fénix, x 28. Mindoro I.: Mindoro Oriental Pr., Batangas Channel (?), Santos 571, 31 xii 36, Puerto Galera, Alcasid 3126, iv 34. Leyte Pr., Biliran I., McGregor P20, vi 14. Bohol I., Cabasihan, Franco 27347, vi–viii 18. Palawan Pr., Palawan I., Puerto Princessa, McGregor, x 25. Sulu Pr., Sibutu I., Abbott, 19 ii 57 (BISH), Turtle Islands, Taganak I., Abbott, 23 ii 57 (BISH), Pearl Bank, Kienholz, x 28. MARIANAS ISLANDS. Saipan I., Kruckeberg, 3 vii 45 (MICH), Guam I., Thompson, 1912. MALAYA. Singapore, Holtum, 1928–30, Panggol, Burkill, 14 i 22. INDONESIA. Java: Djakarta, Hoorn I., Setchell JH579, v 29, Pangendoran, Setchell JP545, v 29. Bali: Sanoer, Setchell BS146, vi 29, Kampoengan, Setchell BK647, 19 vi 29.

Halimeda macrophysa Asken.

PHILIPPINES. Sulu Pr., Turtle Islands, Taganak I., Abbott, 24 ii 57 (BISH).

Halimeda micronesica Yamada

PHILIPPINES. Sulu Pr., Tawitawi Group, Tawitawi I., Abbott, 15 ii 57 (BISH).

Halimeda opuntia (L.) Lamour.

PHILIPPINES. Luzon I.: Cagayan Pr., Calayan I., McGregor, 1903; Quezon Pr., Alabat I., Santos 793, 20 x 37; Camarines Norte Pr., Basiad, Yates, xii 16. Catanduanes Pr., Catanduanes I., Ramos and Edaña, vii–ix 28. Mindoro I.: Mindoro Oriental Pr., Batangas Channel, Santos 566, 31 xii 36. Leyte Pr., Biliran I., McGregor, vi 14. Negros I.: Occidental Negros Pr., Baliangao, Manacop 5118, iii 36. Palawan

Pr., Palawan I., Taytay, Merrill 9141, Puerto Princesa, McGregor, x 25, Balabac I., Abbott, 1 iii 57 (BISH). Sulu Pr., Tapul Group, Siasi I., Abbott, 28 i 57 (BISH), Laminusa I., Abbott, 29 i 57 (BISH), Tawitawi Group, Tawitawi I., Abbott, 30 i 57 (BISH), Sibutu I., Abbott, 17 ii 57 (BISH), Turtle Islands, Taganak I., Abbott, 23 ii 57 (BISH), Sitankai Reef, Yates 36229, x 19. MARIANAS ISLANDS. Guam I., Radin, viii 45. MALAYA. Singapore, Holtum, 1928-30. INDONESIA. Sunda Strait, Teysman. Java: Djakarta, Hoorn I., Setchell *JH580*, v 29, Panganan, Setchell *BP54*, 17 vi 29. Bali: Boeileleng, Pullai 382c, vii 33, Sanoer, Setchell *BS143*, 7 vi 29, Kampoenan, Setchell *BK8*, 9, 641, 651a, 1 vi 29, Panganan, Setchell *BP54*, 17 vi 29.

Halimeda tuna (E. and S.) Lamour., v. *tuna*

PHILIPPINES. Batanes Pr., Batan I., Ramos 80122, vi-vii 30. INDONESIA. Bali: Oie Yong Seng *B191*, 1929-30.

v. *platydisca* (Dec.) Bart.—INDONESIA. Boeileleng, Pullai *BB382*, vii 33, Setchell *BB102*, 19 vi 29, Kampoenan, Setchell *BK649*, vi 29.

Halimeda velasquezii Taylor

PHILIPPINES. Luzon I.: Cagayan Pr., Sta. Ana, Velasquez 2379, 17 vi 50.

Codium Stackhouse, 1797

Codiums of Indonesia have been published upon by the Gepps (1911) and those of the Philippines by Gilbert (1947, 1961). Since Dr. P. C. Silva may be expected to review them in due time in monographic fashion together with other western Pacific specimens, probably with considerable change in species delimitation, no further treatment is appropriate at this time. The Gepps recognized 6 species from the Indonesian area and the Sulu Archipelago; Gilbert (1961) recognized 12 from the Philippines, including all the Indonesian species except the very small Borneo Bank species, *C. petaloideum* A. & E.S. Gepp.

PHAEOPHYCEAE

To judge by the Siboga expedition reports this group, with the exception of a very few genera, is ill-represented in the area from which

the materials available to me have come. It seems very improbable that the representation is adequate, though in truth the variety of Phaeophyceae is not great in the tropics, but it is probably as complete as that of the other major groups. In the present case the genus *Sargassum*, which appears to be best represented in the collections, has been put aside for lack of authentic material for comparison. A special study has been made of the genus *Turbinaria* (Taylor, 1964, 1966), and its distribution recorded in a far more detailed way than would have been possible here. The genus *Padina*, also frequently encountered, was studied several years ago by Dr. Francesca Thivy, and the writer hesitates to draw heavily on her unpublished dissertation, though many of her determinations are incorporated. Delicate forms like *Ectocarpus* were commonly too ill-preserved for determination, and in general small types were entirely unrepresented in the collections.

DICTYOTALES

DICTYOTACEAE

Dictyota Lamouroux, 1809

Materials of *Dictyota* from this area are relatively scanty, and often seem dwarfed; in any case they do not fall readily into distinct species groups. Plants of the genus are often variable in form, and require great care in the field to search out fully developed specimens. One may assume something less than adequacy in this respect, since Setchell is the only fully qualified phycologist whose collections are largely represented (and even so, chiefly by native assistants) in this report. It is remarkable that this Pacific area does not appear to have developed any particularly distinctive species of *Dictyota*.

Dictyota bartayresii Lamour.

PHILIPPINES. Mindoro I.: Mindoro Oriental Pr., Puerto Galera, Santos 563 (*prox.*), 31 xii 36. Palawan Pr., Balabac I., Calendorang Bay, (apices acute and perhaps a distinct entity), Abbott, 1 iii 57 (BISH), Gnat Reef (apices obtuse), Abbott, 4 iii 57 (BISH). Sulu Pr., Turtle Islands, Abbott, 23 ii 57 (BISH).

Dictyota cervicornis Kütz.

PHILIPPINES. Palawan Pr., Balabac I., Abbott, 2 ii 57 (BISH).

Dictyota dichotoma (Huds.) Lamour.

PHILIPPINES. Luzon I., Pangasinan Pr., Hundred Ids., Santos 1158, 9 v 38. Palawan Pr., Balabac I., Abbott, 1 iii 57 (BISH). Sulu Pr., Siasi Group, Laminusa I., Abbott, 29 i 57 (BISH). Tawitawi I., Abbott, 12 ii 57 (BISH).

Dictyota linearis (C. Ag.) Grev.

PHILIPPINES. Luzon I.: Pangasinan Pr., Hundred Ids., Santos 1160, 9 v 38. Sulu Pr., Turtle Ids., Taganak I., Abbott, 23 ii 57 (BISH).

Padina Adanson, 1763

This genus was reviewed by Dr. Francesca Thivy (1945), but the general results have not been published. Identifications reported here were made on the basis of the Thivy study by Dr. L. W. (Hillis) Colinvaux, and later checked in part by the present writer.

Padina australis Hauck

PHILIPPINES. Luzon I.: Quezon Pr., Tayabas, Curran 11128, iii 08; Bataan Pr., Lamao, Shaw 1089, 30 v 09; Pangasinan Pr., Alominos, Fénix, x 28; Ilocos Norte Pr., Burgos, Bonbon, Blanco 3057, 35. Leyte Pr., Leyte I., Tacloban, McGregor, vi 14. Palawan Pr., Palawan I., Taytay, Merrill 9168, v 13, Balabac I., Mangubat 521, iii-iv 06. Mindanao I.: Misamis Occidental Pr., Balianagao, Manacop 5125, iii 36. INDONESIA. Celebes, Macassar, Setchell M480, 481, 22 vi 29.

Padina boryana Thivy n. sp.

Fig. 2

Plants 3–10 cm tall, thin and papery, with a stupose holdfast and stalk; blade about 100 μ thick near the stalk, of two cell layers, that above at least 0.75 as thick as the lower; upper surface hair zones 1–4 mm broad, those on the lower rudimentary, delimiting narrower sterile zones from broader fertile ones, or absent; tetrasporangia about 120 μ diam, in linear non-indusiate sori in the lower portion of the fertile bands, seldom in a median position; oogonia 60–80 μ diam, in similar indusiate sori; antheridial sori in 1–2 rows. Type specimen coll. W. H. Harvey, no. 1 of Friendly Island Algae, in the herbarium of the New York Botanical Garden.

Padina boryana Thivy n. sp.

Plantae 3–10 cm altae, tenues chartaceaeque stuposae super stipitem et discum basalem, orbiculari-reniformes aut in segmenta flabellata usque ad 4 cm lat. divisae; lamina 2-stratosa, ca. 100 μ crass. prope stipitem, strato superiore aequae crasso ac inferiore vel 0.25 tenuiore. Zonae piliferae superficiei superioris aequaliter evidentes, 1–4 mm distantes, zonae superficiei inferioris plerumque rudimentariae vel nullae. Sori tetrasporangiales non-indusiati, in unicum zonam 0.2–1.0 mm lat. super lineas piliferas superficiei superioris, intervallo distincto (0.2–0.5 mm), plerumque in dimidio inferiore zonarum glabrarum; tetrasporangia ca. 120 μ diam. Sori oogoniales lineares, 0.1–0.8 mm lat., paululum super zonas piliferas superficiei superioris dispositi, indusio persistente, oogoniis maturis 60–80 μ diam. Sori antheridiales in zonis fertilibus omnibus in 1 vel 2 seriebus, 0.2–0.5 mm lat., aut parce aggregati, plus quam 0.2 mm supra lineas piliferas. Specimen typicum (tetrasporacum) legit W. H. Harvey, no. 1 in Insulis Amicorum, Polynesia, conservatum in herb. Hort. Bot. Neo-Eborascensis.

PHILIPPINES. Luzon I.: Cagayan Pr., Babuyan Ids., Calayan I., n.c., ix 03; Quezon Pr., Baler, Edaña 5128, iii 39, Polillo, Robinson 6887, viii 09; Catanduanes Pr., Catanduanes, Ramos and Edaña 77621, vii-ix 28. Panay I.: Antique Pr., Semirara Ids., Pasal Pt., Alcasid 6921, iii 40. Palawan Pr., Balabac I., Abbott, 4 iii 57 (BISH). Sulu Pr., Jolo I., Bartlett 16042, 16 ix 35 (MICH). INDONESIA. Bali: Kampoengan, Singaraja, Setchell BK20, 19 vi 29, Patas, Setchell BP349, 1929. Amboina: Robinson 2395, vii-viii 13.

These are plants which would hitherto have passed under the name of *Padina commersonii* Bory (1829:144). The history of this name is confused. Bory used it for Mauritius material which he mistakenly identified with *Zonaria pavonia* (L.) C. Ag., var. *tenuis* C. Agardh from the Marianas Islands (1824:263), the type of which seems actually to have been a *Pocockiella*. Of this Bory appears not to have been aware, but thought it a *Padina* as, of course, was the parent species (J. G. Agardh 1882: 119, as *Zonaria*; Papenfuss 1943:467, as *Pocockiella*). Bory described his plant, but based it on *Zonaria pavonia* var. *tenuis*. Not being able to use the name *tenuis* because of his own *P. tenuis* (Bory, 1827:590), a different thing, he proposed the new name *P. commersonii*, citing *Zonaria pavonia* var. *tenuis* in synonymy. The basis of this new name is, then, the type of var. *tenuis*, and the species name *commersonii* goes

Pocockiella Papenfuss, 1943*Pocockiella variegata* (Lamour.) Papenf.

PHILIPPINES. Palawan Pr., Balabac I., Abbott, 1 iii 57 (BISH). Sulu Pr., Tawitawi Group, Tawitawi I., Abbott, 13 ii 57 (BISH). Doubtless common and widely distributed in the Philippines and Indonesia, but commonly inconvenient to collect.

PUNCTARIALES
PUNCTARIACEAE

Chnoospora J. Agardh, 1847.*Chnoospora minima* (Hering) Papenf.

PHILIPPINES. Luzon I.: Pangasinan Pr., Hundred Islands, Santos 1159, 9 v 38.

Hydroclathrus Bory, 1826*Hydroclathrus clathratus* (Bory) Howe

PHILIPPINES. Luzon I.: Pangasinan Pr., Hundred Islands, Santos 1161, 9 v 38. Palawan Pr., Balabac I., Abbott, 1 iii 57 (BISH), Gnat Reef, Abbott, 4 iii 57 (BISH). MARIANAS ISLANDS. Guam I., Newhall, 1900–01, Nelson 508, 18.

FUCALES
CYSTOSEIRACEAE

Cystophyllum J. Agardh, 1848*Cystophyllum muricatum* (Turn.) J. Ag.

INDONESIA. Celebes: Macassar, Setchell M509, 23 vi 29. Bali: Sanoer, Setchell BS260, 15 vi 29.

Hormophysa Kützinger, 1843*Hormophysa triquetra* (L.) Kütz.

PHILIPPINES. Luzon I.: Bataan Pr., Lamo, Shaw 1095a, 30 v 11, Limay, Shaw 1110, 24 iv 11; Pangasinan Pr., Alominos, Fénix, x 28; La Union Pr., San Fernando, Fénix 13015, xii 10. MALAYA. Singapore, St. Johns I., Corner 22188, 31 xii 29, Birtwhistle, v 28. INDONESIA. Anambas Islands, Tandjong Padang, Henderson 20434, 16 iv 28. Bali: Sanoer, Setchell BS254, 11 vi 29. Celebes: Macassar, Setchell M483, 23 vi 29.

SARGASSACEAE

Sargassum C. Agardh, 1820

The bulk of available *Sargassum* material from this area far exceeds that of any other genus of Phaeophyceae. Unfortunately, without prolonged access to authentic materials identification of most of it seems impracticable. A few particularly notable specimens, however, are included here with considerable confidence respecting their identity.

Sargassum crassifolium J. Ag., prox.

MARIANAS ISLANDS. Guam I., Nelson 511, 1918.

Sargassum cristatum J. Ag., prox.

PHILIPPINES. Luzon I.: Pangasinan Pr., Hundred Islands, Santos 1167, n.d. Perhaps Grunow correctly (1915) reduces this to synonymy under *S. aemulans* Sond.

Sargassum duplicatum J. Ag.

PHILIPPINES. Mindoro I.: Mindoro Oriental Pr., Puerto Galera, Bartlett 13797, 12–17 v 35 (WRT). MARIANAS ISLANDS. Guam I., Thompson, 1912. INDONESIA. Java: Palabuhan Bay, Martens (WRT), Zaandbai, Möller, v viii 97 (WRT). Amboina: Robinson 576, vii–ix 13 (to represent *Acetabulum marinum* of Rumphius), (filed as *Turbinaria*, NY). NEW GUINEA. North-east New Guinea, Cape Creten east of Lae, Keefe, 1944 (WRT).

Sargassum polycystum C. Ag.

MARIANAS ISLANDS. Guam I.: Newhall, 1900–01, Clemens, 27 xi 11, Thompson, 1912.

Sargassum sandei Reinb.

PHILIPPINES. Mindoro I.: Mindoro Oriental Pr., Puerto Galera, Bartlett 13980, 12–15 v 35 (WRT).

Turbinaria Lamouroux, 1828

This genus has recently been reviewed (Taylor, 1964, and in press, 1966) and specimens from the sources contributing to this present paper are cited there in a more comprehensive fashion than is possible here. However, a few additions are included, since they apply particularly to the Philippines. It will be seen

by the papers mentioned that *T. ornata* is particularly common and widespread, ranging from northeastern Africa to Malaya and Taiwan, south past Queensland perhaps to Tasmania, and throughout the western Pacific to Hawaii, so that citation of specimens, particularly from the Philippines and the Marshall Islands, had to be restricted to those adequately delimiting the range. However, *T. decurrens* seems more unusual and is much less common in collections, though ranging from Madagascar, Hainan, and southern Luzon to the Solomon Islands. One may expect *T. conoides* from Kenya and Tanganyika in east Africa to India, Malaya, Luzon, thence south and east to the Tonga and Samoan island groups. It is next after *T. ornata* in frequency of collection. So far *T. luzonensis* Taylor is known only from Luzon. *Turbinaria condensata* Sonder, described from somewhere in the China Sea, is definitely known from Somalia and Kenya on the west to Malaya, Luzon, Guam, and western Australia.

Turbinaria conoides (J. Ag.) Kütz.

PHILIPPINES. Sulu Pr., Tawitawi Group, Tawitawi I., Tjititji Reef, Abbott, 15 iii 57 (BISH).

Turbinaria decurrens Bory

PHILIPPINES. Sulu Pr., Turtle Islands, Taganak I., Abbott, 24 ii 57 (BISH).

Turbinaria ornata (Turn.) J. Ag.

PHILIPPINES. Palawan Pr., Balabac I., Pasig Bay, Abbott, 1 iii 57 (BISH), Sibutu I., Abbott, 19 ii 57 (BISH), Turtle Islands, Taganak I., Abbott, 24 ii 57 (BISH). Sulu Pr., Cagayan Sulu I., Abbott, 27 ii 57 (BISH).

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A New Camallanid Nematode from Hawaii

ELMER R. NOBLE¹

ABSTRACT: *Spirocamallanus istiblenni* n. sp. is described from the intestine of *Istiblennius zebra*, a tidepool fish at Oahu, Hawaii. Female worms average 21.5 mm long, and the adult female:male length ratio is 1.44:1.0. The chief diagnostic characters include a reduced posterior ovary, a male caudal papillae pattern of six preanal and three postanal, a spicule length ratio of 3:2, and an H-shaped arrangement of the anterior excretory canal system. The buccal capsule possesses 13–14 spiral thickenings. The possible evolutionary significance of the posterior ovary is mentioned; a list of other parasites of this host and ecological considerations are included.

DURING THE MONTHS from November 1962 to April 1963 I collected tidepool fishes at several points around the island of Oahu, Hawaii and examined them for protozoan, helminth, and arthropod parasites. Among the fishes were 50 specimens of *Istiblennius zebra*, half of which contained, in their intestines, nematodes belonging to the genus *Spirocamallanus*. A detailed study of this worm shows it to be a new species, and requires a modification of presently accepted diagnostic characteristics of the genus and of the family Camallanidae.

THE HOST AND ITS ENVIRONMENT

Istiblennius zebra, family Blenniidae, lives as an adult among rocks along the shore and is often abundant in small tidepools. Temperature changes in the water of these pools varied (during the days that I was there) between 22.6 C to 34.8 C, and salinity changes varied between 33.68‰ to 36.20‰. Eggs of the fish are deposited in the pools, and larvae migrate to open water off shore. Young fish return to the rocky shores where they spend the remainder of their lives. Adult fish feed primarily on a precipitated organic detritus called "leptopel" which appears to be chiefly of

algal origin. Snails, green algae, and ostracods were occasionally found in the stomach. Other organisms in the pools were plankton (copepods, ostracods, crustacean larvae, juvenile snails, nematodes, unicellular algae, filamentous algae, diatoms), fish (*Bathygobius fuscus*, *Abudefduf sordidus*, other small fish), sea urchins, sea anemones, shrimps, colonial ascidians, small nudibranchs in clumps of algae, annelids, snails (*Littorina picta*, *L. pintado*, *Nerita neglecta*, *Morula nudus*, *Cerithium* sp., and others), and algae (*Lyngbya majuscula*, *Valonia aegagropila*, and other species). When the host fish were found on coral reefs they were associated with the multitudinous fishes and other organisms common to the reefs.

THE PARASITE

Spirocamallanus istiblenni n. sp.
(Figs. 1–10)

HOST: *Istiblennius zebra* (Vailland & Sauvage).

SITE OF INFECTION: Intestine (of 25 out of 50 hosts).

LOCATION: Marine tidepools at Oahu, Hawaii.

SYNTYPES: U. S. Nat. Hist. Mus. Helm. Coll. Nos. 32914 (male), 32915 (female).

DESCRIPTION: A tabulation of measurements, based on nine females and five males, is given in Table 1.

The chief features that distinguish *Spirocamallanus istiblenni* from other described species are the presence of a posterior ovary, the caudal

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TABLE 1
MEASUREMENTS OF *Spirocamallanus istiblenni*

	MALE (MM)	FEMALE (MM)
Body length	14.900	21.500
Body width	0.221	0.326
Anus to posterior end	0.166	0.177
Excretory pore to anterior end	0.400	0.400
Vulva to anterior end	—	8.200
Buccal capsule, length	0.075	0.077
Buccal capsule, width	0.072	0.077
Esophagus (muscular) length	0.325	0.397
Esophagus (glandular) length	0.485	0.588
Nerve ring to anterior end	0.208	0.220
Right spicule, length	0.274	—
Left spicule, length	0.184	—
Number preanal papillae	6	—
Number postanal papillae	3	—
Anterior ovary length	—	6.100 (max. 10.0)
Posterior ovary length	—	0.850 (max. 01.0)
Mature ova in anterior ovary	—	0.011 × 0.015
Ova in posterior ovary	—	0.008 × 0.010

papillae pattern (six preanal, three postanal) in the male, the spicule length ratio of 3:2, the female:male body length ratio of 1.44:1, and the arrangement of the anterior excretory canals. These features, and others, will be discussed briefly.

The mouth is circular, without lips. An *en face* view of a preserved specimen shows that the anterior surface of the buccal capsule pos-

sesses eight lateral projections, and is surrounded by inconspicuous folds (Fig. 1). The orange-brown buccal capsule (Fig. 2) is lined with 13 or 14 spiral thickenings. Between the buccal capsule and the body wall are located four elongated buccal sinuses, two dorsal and two ventral in position. These sinuses are probably

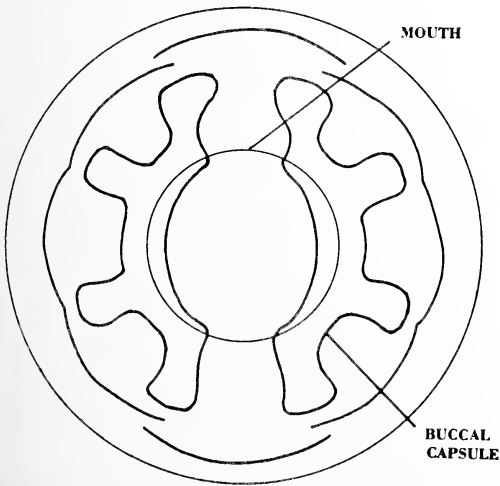


FIG. 1. *En face* view. The outer surface around the mouth is smooth.

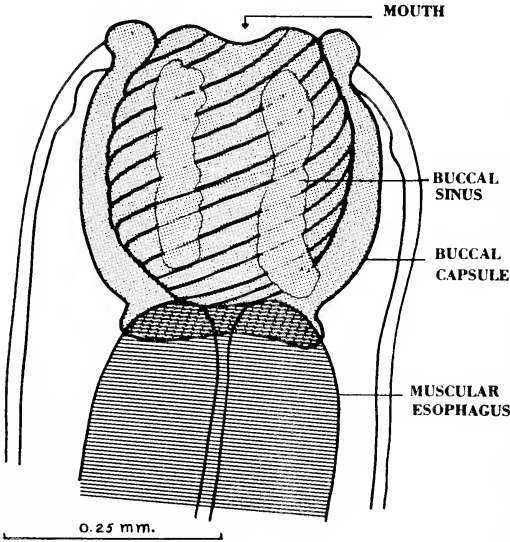


FIG. 2. Lateral view of head to show the buccal capsule and position of buccal sinuses.

a part of the osmoregulatory system, but connections between them and the excretory canals were not clearly distinguished.

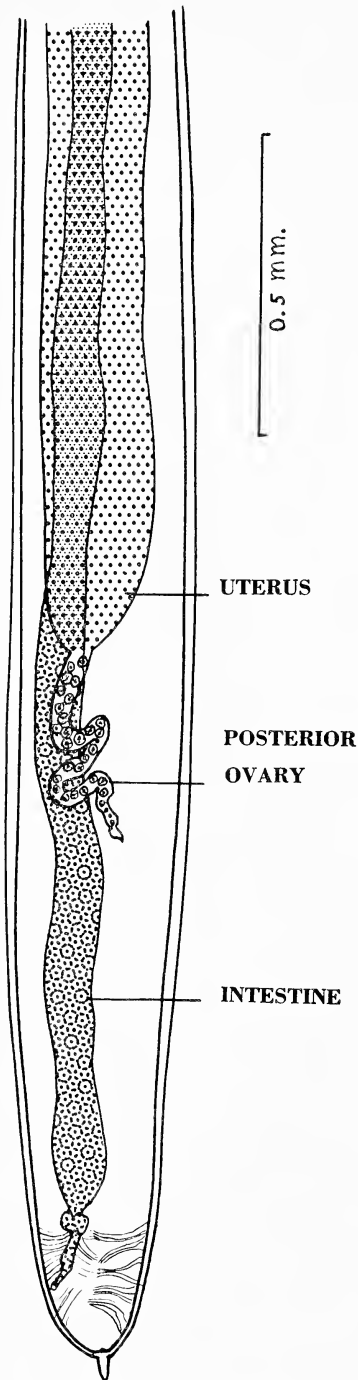


FIG. 3. Posterior end of a female worm, showing the posterior vestigial ovary.

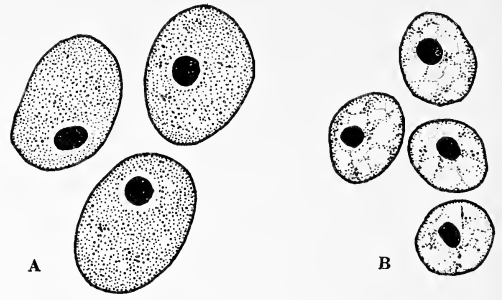


FIG. 4. *A*, Ova from an anterior ovary; *B*, ova from a posterior ovary. Immature ova in an anterior ovary appear similar to those in *B*.

One of the important diagnostic characteristics of the family Camallanidae, as listed in the literature, has been a blind posterior branch of the uterus. The posterior ovary in *Spirocamallanus istiblenni* (Fig. 3) is normally much shorter than the anterior ovary, and it contains cells that appear similar to the immature ova in the first portion of the anterior ovary (Fig. 4). The posterior ovary is probably vestigial, and thus appears to represent a last stage in the evolutionary progression toward the elimination of one ovary. The large, coiled, anterior ovary, plus the oviduct, reaches a maximum length of about 10 mm, or half of the total body length. The oviduct narrows before it enters the expanded seminal receptacle (Fig. 5), which itself narrows before entering the large, thin-walled uterus. At this latter junction the walls contain glandular cells. In one of the nine female worms the long, functioning ovary is not anterior in position, but is posterior, and the seminal receptacle expands to form the posterior horn of the uterus.

The male caudal papillae are grouped as shown in Figure 6, and the alae curve anteriorly to meet ventrally. The two spicules bear a length ratio of 3:2 (Figs. 6, 7). In both male and female worms the lower part of the intestine and the rectal gland are supported by conspicuous muscle fibers (Figs. 6, 8). In the male the anus is surrounded by four small papillae (adanal), a condition not uncommon in this genus. The posterior finger-like tip of the body has from zero to three minute projections.

Two excretory canals run the entire length of the worm, and join at about the level of the glandular esophagus to form an excretory sinus

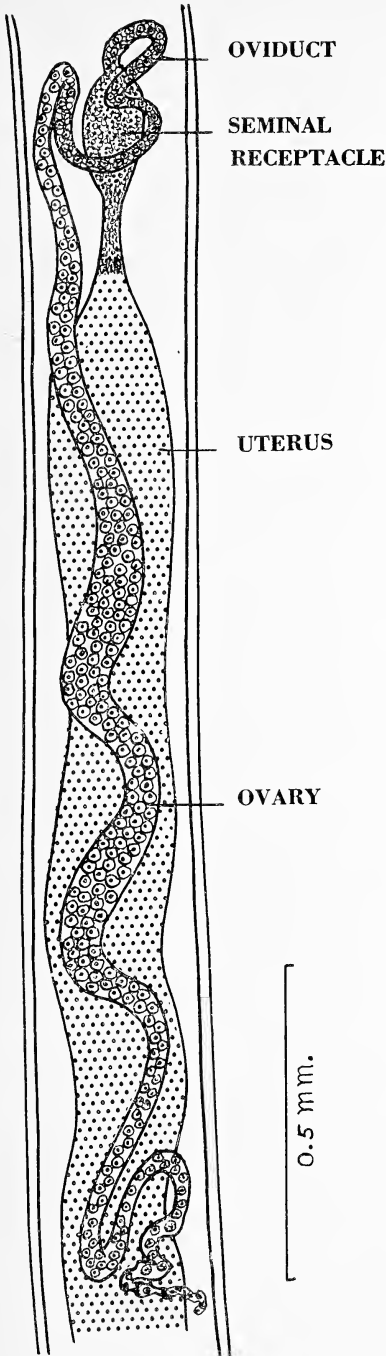


FIG. 5. The anterior ovary, oviduct, and seminal receptacle.

(with a large sinus nucleus) that opens to the exterior by a short excretory duct (Fig. 9). The vulva is located just anterior to the middle of

the female body, and the vagina extends posteriorly, for about 1.3 mm, to the uterus (Fig. 10). The distal portion of the vagina has a thick, muscular wall and is about 0.4 mm long.

DISCUSSION

A number of copepods collected in the tide-pools with *Istiblennius zebra* were examined for larval stages of the parasite, but no larvae were

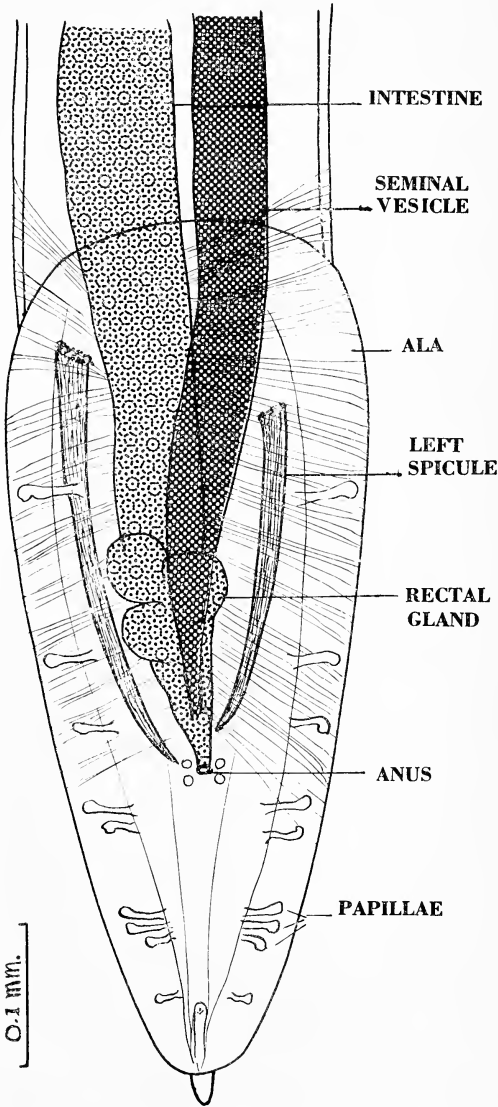


FIG. 6. Posterior end of a male worm, ventral view. Note particularly the number and arrangement of papillae and relative sizes of the spicules.

found. The average number of worms in infected hosts was 5, the maximum was 30. The population of parasites, therefore, was sufficiently dense to provide numerous larvae in the water. All of the mature female worms were filled with larvae in all stages of development, including actively moving forms ready to leave the mother. The absence of parasites in the copepods is difficult to explain, since copepods are presumably the intermediate hosts. The season of the year might be a factor, but probably not enough copepods were examined.

There is no evidence that the worms are pathogenic to the host. Any consideration of parasite-host relationships should include at least a notice of the total parasite fauna. Other parasites found in the 50 hosts examined were:

On the gills: *Trichodina* (closely similar to *Paratrichodina obliqua*), *Gyrodactylus* sp., metacercariae, and a microcotyline monogenetic trematode.

In the gall bladder: the myxosporidians, *Zschokkella* and *Ceratomyxa*.

In the muscles: metacercarial cysts.

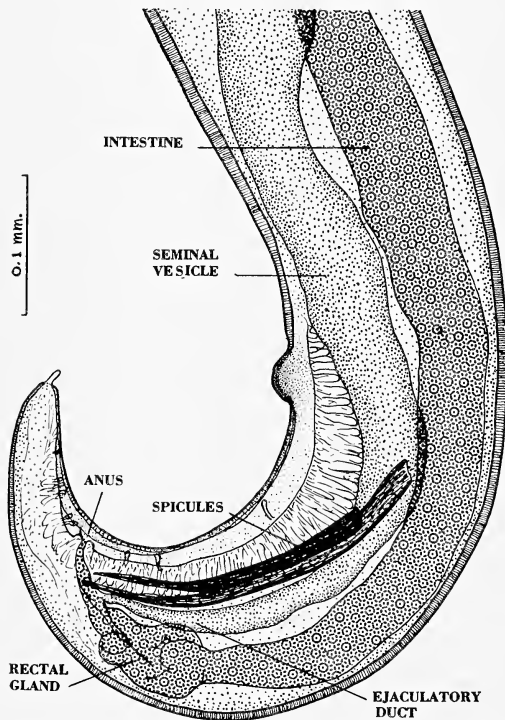


FIG. 7. Posterior end of a male worm, lateral view.

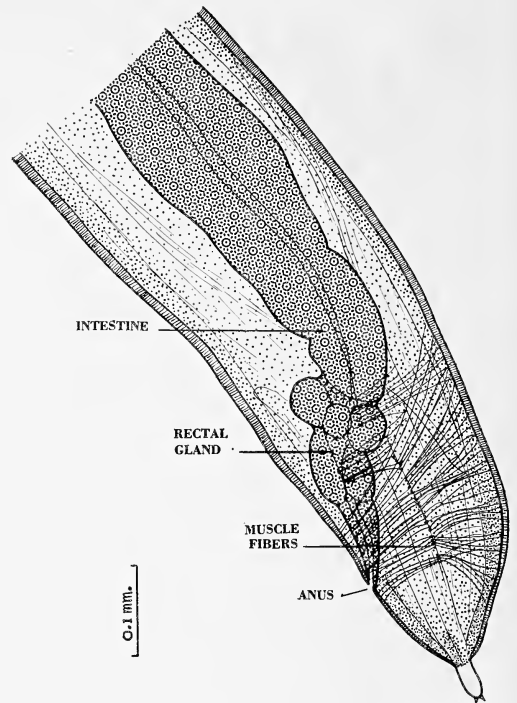


FIG. 8. Posterior end of a female worm, lateral view.

In the digestive tract: metacercarial cysts (in only one host).

The paucity of parasites in the intestine is probably correlated with the host's habit of feeding primarily on an organic detritus. *Spirocamallanus istiblenni* obviously does not have much competition for space and nutrients except that provided by its host.

In 1952 Olsen erected a new genus, *Spirocamallanus*, to accommodate 17 species of *Procamallanus* characterized by spiral thickenings inside the buccal capsule. Ali (1960) has pointed out that within the genus *Procamallanus* there are species with "comb-like chitinous plates," finger-like projections, "golf club shaped projections," "knob-like structures," transverse thickenings, and other modifications of the buccal capsule wall. Ali believes that the use of spiral thickenings as the sole basis of distinction is not warranted, and that the spicule pattern in the male offers morphological variations that are more sharply defined. Some worms do not possess spicules, in others there are one or two, and in the latter group the

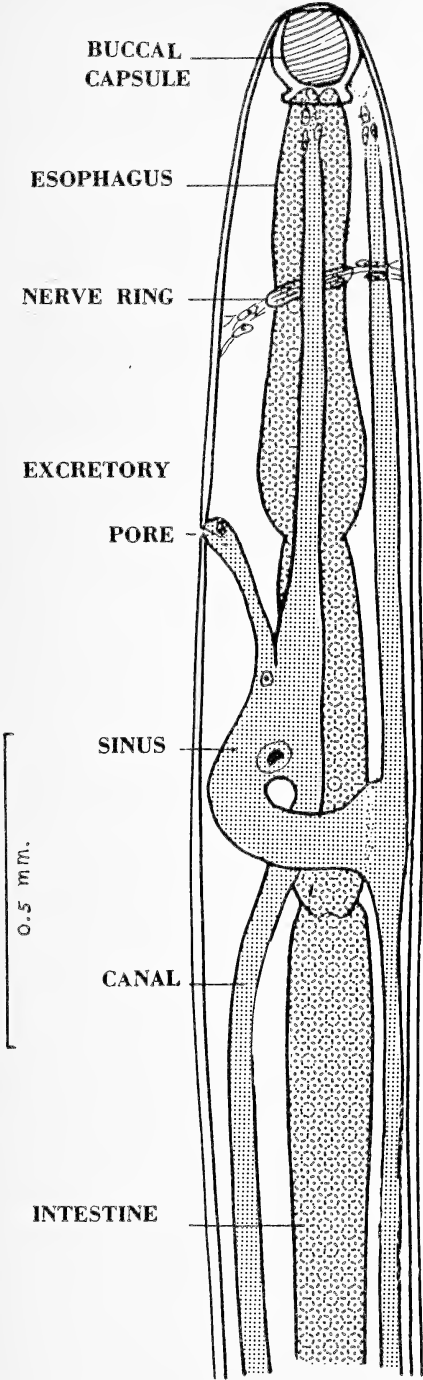


FIG. 9. Dorsal view of anterior end to show excretory canals, sinus, and excretory pore.

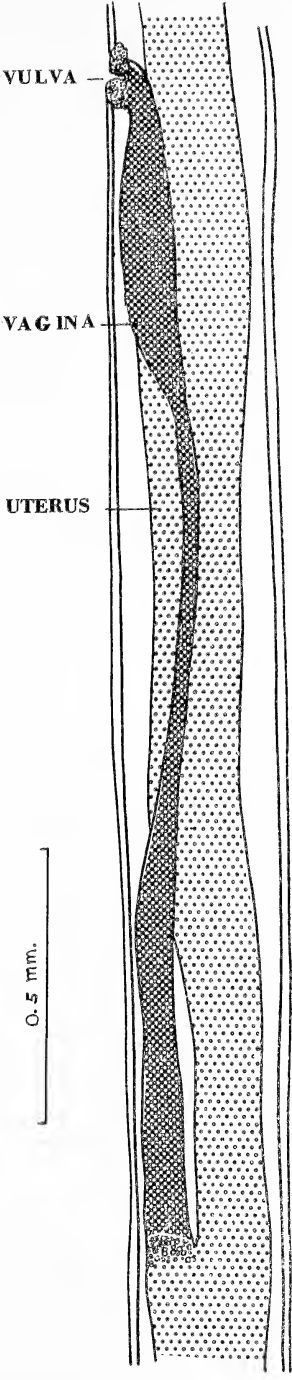


FIG. 10. An area just anterior to middle of female body, to show the vulva, vagina, and connection with uterus.

TABLE 2

COMPARISON OF *S. istiblenni* WITH TWO OTHER SPECIES OF *Spirocamallanus*

FEATURE	<i>S. istiblenni</i>	<i>S. spiralis</i>	<i>S. pereirai</i>
Posterior ovary	present	absent	absent
Female:male body length ratio	1.44:1	1:3	1.4:1
Caudal papillae (male)	9 pair	7-9 or more	9 pair
No. buccal capsule spirals	13-14	12	14
Right spicule, length	0.27 mm	0.15 mm	0.21 mm
Left spicule, length	0.18 mm	0.1 \pm mm	0.21
Length ratio of spicules	3:2	1.5:1	2:1

spicules are equal or unequal in length. Using these characteristics, Ali has created four subgenera: *Aspiculus*, *Monospiculus*, *Isospiculus*, and *Procamallanus*. One objection to using this basis of classification is that a male worm must be found before the female can be specifically identified. Also, Olsen (1952) has raised some doubt as to the existence of males with only one spicule. Yeh (1960) has dealt with the problem of varieties of buccal capsule linings by using them as bases for a "reconstruction of the genus *Camallanus*." He created two new subfamilies: Camallaninae and Procamallaninae. The latter consists of two genera: *Procamallanus* (Baylis, 1923) with a smooth buccal capsule lining, and *Spirocamallanus* Olsen, 1952, with spiral thickenings. I am inclined to agree with Yeh.

Spirocamallanus istiblenni appears to be most similar to *S. pereirai* (Annereaux, 1946) and *S. spiralis* (Baylis, 1923). Some comparative features are listed in Table 2.

In the light of the descriptions presented in this paper the diagnostic characteristics of the family Camallanidae and of the genus *Spirocamallanus* should include the statement that the posterior horn of the uterus is usually blind,

but that a second, posterior, reduced ovary may be present.

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Foods of Rodents in the Hamakua District, Hawaii¹

HARRY T. KAMI²

ABSTRACT: The food habits of *Rattus exulans*, *R. rattus*, *R. norvegicus*, and *Mus musculus* captured in sugar cane fields, in gulches adjacent to cane fields, and in areas of human habitation, were determined from the stomach contents of 1205 rodents collected in 12 consecutive monthly samples. In cane fields the diet of *R. exulans* and *R. rattus* was primarily the internodes of sugar cane, while *Mus* fed principally on insects and grass seeds. In gulches *R. exulans* subsisted mainly on sugar cane, but *R. rattus* fed heavily on grass stalks and fruits. *Mus* from this habitat consumed *kukui* nuts and insects to a large extent, while the few *R. norvegicus* found here took a variety of foods. The foods of *R. rattus* and *R. norvegicus* captured near human habitations consisted mainly of garbage, other waste materials, and mixed livestock rations.

NUTRITION is a primary requirement for the support of animal populations, and its quality is considered by some ecologists to be the ultimate factor which controls the growth or decline of such populations. Hence, knowledge of food habits is an important element in the understanding of rodent ecology. In Hawaii early investigations by Caum (1922), Spencer (1938), and Doty (1945) provided basic information for their programs directed toward control of rodents which damage sugar cane.

The present investigation was undertaken as part of extensive research on the reservoirs and vectors of bubonic plague. Three species of rats, *Rattus rattus* (L.), *R. norvegicus* (Berkenhout), and *R. exulans* (Peale), and a mouse, *Mus musculus* L., make up the rodent complex of the Hamakua district on the northeast coast of the island of Hawaii. Because plague bacilli have been detected many times in humans, rodents, and rodent fleas in the area extending from the village of Kukuihaele on the west to that of Paauhau on the east, trapping effort for rodent collections was concentrated within that area.

I wish to thank the Rodent Surveillance and Control Crew, Department of Health, Honokaa, supervised by Mr. R. Baker, for rodents from the many villages scattered throughout the district; Dr. Kaoru Noda and Dr. Satyu Yamaguti, University of Hawaii, for identification of nematodes; Dr. Dale H. Habeck, University of Florida, for identification of insects; and Dr. P. Quentin Tomich for his valuable suggestions during the course of the work and for his critical reading of the manuscript.

DESCRIPTION OF SELECTED HABITATS

Sugar Cane Fields

Permanent trap lines were established in sugar cane fields which varied in crop age from recently planted seedlings to mature cane, ready for harvest. In fields of young cane the area between the rows is bare of weeds and other cover. After a time, the ground is often overgrown by seed-producing forbs and grasses, and so littered by the fallen leaves and stalks of cane that penetration of the field is nearly impossible.

Gulches

Trap lines were also established in two gulches, Ouhi gulch near Paauhau and an unnamed gulch adjacent to cane fields near Waipio Valley. The section of Ouhi gulch studied

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² Plague Research Unit, Department of Health, State of Hawaii.

separates a cane field from a waste grassland. Throughout the area from which rodents were trapped, large Java plum trees (*Eugenia cumini*) and *kukui* trees (*Aleurites moluccana*) form a forest-like overstory. In the understory there are *ti* plants (*Taetsia fruticosa*), coffee shrubs (*Coffea* sp.), and a restricted variety of other species. The floor of this gulch is formed of large exposed boulders and is subject to occasional, torrential runoff.

Thick stands of false ironwood (*Casuarina* sp.) predominate in the gulch near Waipio Valley. Scattered growths of *kukui* and guava (*Psidium guajava*) trees, and of *ti*, as well as patches of palm grass (*Setaria palmifolia*) and panicum grasses (*Panicum purpurascens*, *P. maximum*) are found along the slopes. The floor of this short gulch is not eroded and is densely matted with *honohono* (*Commelina nudiflora*), panicum, and palm grasses.

Areas of Human Habitation

In residential areas, consisting mainly of rural villages, traps were placed in or about houses, storage sheds, garages, stone fences, hedges, orchards, pig and cattle pens, and chicken coops.

METHODS AND PROCEDURES

The stomachs of rodents caught by snap-traps were removed in the laboratory and preserved in 70% isopropyl alcohol. Contents were weighed to the nearest 0.1g on a triple beam balance, and then sorted and spread evenly in a petri dish. A grid of 1 cm² units, drawn on a card, was placed beneath the dish to aid in estimating the percentages of different items found in the stomach. Weights and percentages of these items were the only quantitative measurements taken.

Examination of the food materials was made with the aid of a dissecting microscope. Items not easily distinguished were placed on a piece of cheesecloth and washed with a jet of water. Hulls of certain grass seeds and stalks were washed and dried to make identification possible. Identifications were frequently made by direct comparison with sample items gathered from the various trapping areas. (A check list of botanical names of plants used by rodents as food will be found at the end of this article.)

Because coconut was used as bait in snap-traps, stomachs of rodents which had fed exclusively on coconut were not included in the tabulations. Rodents caught in a 3.5-acre tract of waste grassland adjacent to a sugar cane field were treated as being caught in the cane field, because stomach examinations showed contents similar to rats caught in cane fields and also because of the small sample size of rats captured in the grassland.

Trapping was conducted once a month for a four-day period from July 1963 to June 1964.

RESULTS

Cane Fields (see Table 1)

Rattus norvegicus: Only one specimen was obtained from the cane fields; insect fragments were the only dietary item. This animal was not included in Table 1.

Rattus exulans: The principal food of cane field *R. exulans* was sugar cane, which occurred in 68.2% of the rats and amounted to 67.2% of the food materials. Foods of secondary importance were seeds and stalks of grasses, found in 21.3% of the animals and constituting 15.1% of the volume. Insects, including adults, larvae, and egg masses, contributed 6.0% to the food materials.

In most cases, identification of these insects was possible only as ground-inhabiting Coleoptera or Orthoptera because the hard chitinous exoskeleton was masticated into fine fragments beyond exact recognition. However, the larvae of craneflies (Tipulidae) and small moths (Tineidae), and the adults of the sugar cane mealy bug (*Saccharicoccus sacchari*) and of the sugar cane weevil (*Rhabdoscelus obscurus*), and the eggs of the mealy bug were identified below the ordinal level. Larvae and egg masses were often found mixed with other food items, but no relationship between these insects and any particular food item was found.

The pulp and seeds of guava fruits were utilized by 4.8% of the animals and formed 3.5% of the volume. Other food materials included *kukui* nuts, animal flesh, earthworms, slugs, and materials which could not be identified. These items amounted to 8.1% of the volume.

TABLE 1
STOMACH CONTENTS OF RODENTS CAPTURED IN CANE FIELDS

FOOD ITEMS	<i>Rattus exulans</i>			<i>Rattus rattus</i>			<i>Mus musculus</i>		
	NO. EXAMINED: 359			NO. EXAMINED: 34			NO. EXAMINED: 345		
	FREQUENCIES NO.	%	VOL. %	FREQUENCIES NO.	%	VOL. %	FREQUENCIES NO.	%	VOL. %
Fruits and berries	17	4.8	3.5	4	11.8	5.7	2	0.6	0.3
Grass (seeds)	50	14.0	8.6	6	17.6	11.9	132	38.3	32.0
Grass (stalks)	26	7.3	6.5	3	8.8	5.5	8	2.3	3.0
Insect	68*	19.1	6.0	5*	14.7	4.4	56	16.2	7.4
Insect (egg mass)							86	24.9	25.5
Insect (larvae)							31	9.0	5.9
Sugar cane	243	68.2	67.2	21	61.8	59.7	25	7.2	9.8
Nuts	3	0.8	0.7				5	1.4	1.8
Unidentified material	21	5.9	5.9	5	14.7	11.9	24	6.9	10.9
Animal flesh	3	0.8	0.5	1	2.9	0.8	5	1.4	1.8
Other invertebrates (earthworms and slugs)	10	2.8	1.0				7	2.0	1.6

* Includes adults, larvae, and egg masses.

TABLE 2
SUMMER AND WINTER FEEDING PATTERN OF *R. Exulans* CAPTURED IN CANE FIELDS

FOOD ITEMS	SUMMER (APRIL–SEPTEMBER)			WINTER (OCTOBER–MARCH)		
	NO. EXAMINED: 169			NO. EXAMINED: 190		
	FREQUENCIES NO.	%	VOL. %	FREQUENCIES NO.	%	VOL. %
Fruits and berries	10	5.9	3.6	9	4.7	3.8
Grass (seeds)	35	20.7	14.1	13	6.8	3.6
Grass (stalks)	13	7.7	6.4	13	6.8	6.2
Insects	41*	24.3	9.6	25	13.1	2.2
Sugar cane	94	55.6	56.2	147	77.4	77.7
Nuts				3	1.6	1.2
Unidentified materials	14	8.3	8.3	7	3.7	3.9
Animal flesh				1	0.5	0.6
Other invertebrates (earthworms, slugs, etc.)	7	4.1	1.7	4	2.1	0.8

* Includes adults, larvae, and egg masses.

Although heavy feeding on sugar cane was evident throughout the year, its use during the winter period increased 21.8% in frequency and 21.5% in volume. During the summer there was an increase in the consumption of grass seeds and insects (see Table 2). No seasonal changes were observed in the use of fruits. The other food items were too infrequently observed to allow seasonal comparisons.

Rattus rattus: The pattern of food preferences was similar to that of *R. exulans*. Sugar

cane was the primary diet; 61.8% of the animals fed on cane which formed 59.7% of the volume. Grass seeds and stalks were of considerable importance to 26.4% of *R. rattus* and these foods amounted to 17.4% of the diet by volume. The seeds and stalks of *Panicum maximum*, *P. purpurascens*, and *Setaria palmifolia* were preferred to other available grasses by both *R. rattus* and *R. exulans*.

Fruits, mainly guavas, and a few berries of poha (*Physalis peruviana*) and of nightshade (*Solanum nigrum*), constituted 5.7% of the

TABLE 3
STOMACH CONTENTS OF RODENTS CAPTURED IN GULCHES

FOOD ITEMS	<i>Rattus exulans</i> NO. EXAMINED: 146			<i>Rattus rattus</i> NO. EXAMINED: 123			<i>Mus musculus</i> NO. EXAMINED: 25			<i>Rattus norvegicus</i> NO. EXAMINED: 3		
	FRE- QUENCIES			FRE- QUENCIES			FRE- QUENCIES			FRE- QUENCIES		
	NO.	%	VOL. %	NO.	%	VOL. %	NO.	%	VOL. %	NO.	%	VOL. %
Fruits and berries	18	12.3	9.4	41	39.8	30.5				1	33.3	33.3
Grass (seeds)	4	2.7	1.7	14	13.6	10.1	6	24.0	14.6			
Grass (stalks)	30	20.5	17.7	28	27.2	23.2						
Insects	20*	13.7	2.9	5*	4.8	2.2	6	24.0	5.6			
Insects (egg mass)							4	16.0	14.0			
Insects (larvae)							2	8.0	0.6			
Sugar cane	76	52.0	51.8	8	7.8	6.3				1	33.3	21.6
Nuts	8	5.5	6.2	12	11.6	10.7	5	20.0	23.3			
Unidentified materials	11	7.5	7.2	14	13.6	11.5	7	28.0	41.9	2	66.7	45.0
Animal flesh	5	3.4	3.0	6	5.8	5.0						
Other invertebrates (earthworms, slugs, etc.)				1	1.0	0.3						

* Includes adults, larvae, and egg masses.

R. rattus diet. Insects and unidentified materials occurred in uniform frequencies, but the latter items were greater in volume. Trace amounts of rodent flesh and pelage were found in a single specimen. *Kukui* nuts and the lower invertebrates were absent from the diets of *R. rattus* from cane fields. Because of the small sample size, no comparison between summer and winter feeding pattern was made.

Mus musculus: Insects, primarily egg masses, and seeds of *Digitaria henryi*, *Paspalum conjugatum*, and *Panicum maximum* comprised 38.8% and 32.0% respectively of the food materials of *Mus*. Sugar cane, an important source of food for *R. rattus* and *R. exulans*, was of little importance to this species. Only 7.2% of the mice fed on cane and it formed a mere 9.8% of the volume. Unidentified materials constituted 10.9% of the volume. Other food items such as fruits and berries, nuts, animal flesh, and lower invertebrates amounted to 5.5% of the diet. No apparent differences in the feeding pattern between winter and summer were observed.

Gulches (see Table 3)

Rattus norvegicus: The Norway rat was the least abundant rodent in the gulches; only three were captured. Fruit of the Java plum was the

only food item in one specimen, materials in a second rat could not be identified, and the third had eaten 65% sugar cane along with 35% unidentified materials.

Rattus exulans: The major food source of the gulch-inhabiting *R. exulans* was sugar cane. This item occurred in 52.0% of the rodents and formed 51.8% of the food materials. Grass stalks were taken by 20.5% of the rats and amounted to 17.7% of the volume.

In the gulches many animals fed on *kukui* nuts, guava fruits, and berries. These items formed 15.6% of their diets. Although insects were found in 13.7% of the animals, they amounted to only 2.9% of the volume. The remaining 11.9% of the food materials consisted of grass seeds, animal flesh, and unidentified matter.

Rattus rattus: The preferred foods of *R. rattus* in the gulches were seeds and stalks of grass, and guava fruits. These items constituted 33.2% and 30.5%, respectively, of their diet and occurred in 40.8% and 39.8%, respectively, of the animals. Gulch *R. rattus* also fed more on *kukui* nuts than on sugar cane. Nuts were consumed by 11.6% of the animals and amounted to 10.7% of the volume, while cane was eaten by 7.8% of the rodents and amounted to 6.3% of the volume.

Insects appeared in 4.8% of the animals, and contributed 2.2% to the volume. Unidentified materials, animal flesh, and traces of lower invertebrates comprised the remaining 16.8% of the dietary items.

Mus musculus: Insects continued to be one of the major food sources of 48% of the mice taken in this habitat and constituted 20.2% of their diet. *Kukui* nuts, the other item of major importance, though absent from the diet of cane field *Mus*, were consumed heavily by 20.0% of the mice and amounted to 23.3% of the volume.

Grass seeds also were of considerable importance, with 24.0% of the mice feeding on them to form 14.6% of the diet. However, a large portion of foods eaten (41.0% by volume), were materials that could not be identified.

Absent from the diet of *Mus* were fruits and berries, grass stalks, sugar cane, animal flesh, and lower invertebrates, all of which appeared in the cane field *Mus*.

Residential and Other Areas Associated with Human Habitation (see Table 4)

Rattus norvegicus: The diet of Norway rats taken from areas associated with human habitation included materials (60.1% by volume) that could not be identified. This predominance of unidentified materials was attributed to the nature of the food sources (i.e., garbage, chicken feeds, hog swill, garden vegetables,

etc.) associated with this habitat. Norway rats showed no marked preference for other food items, which they ate in considerable variety.

Rattus rattus: Of the food materials of *R. rattus* taken from this area 40% consisted of materials which could not be identified. Grass stalks continued to be of importance, forming 20.9% of the diet. Although more of the rats had fed on guava fruits than on sugar cane, these items differed only slightly in volume. Guava was consumed by 18.2% of the rats and it contributed 10.7% to the total volume, while sugar cane was consumed by 12.7% of the animals and amounted to 11.1% of the volume. Other dietary items consisting of grass seeds, insect forms, nuts, and animal flesh formed the remaining 17.0% of the food materials.

Stomach Parasites

During the course of this project, nematodes were frequently found in the stomach in rats, but infrequently in *Mus*. These nematodes were so numerous in some rats that their stomachs were filled with these parasites. As many as 32 nematodes were found in a stomach. Parasitism was highest among *R. rattus*, with 113 of 312 (36.2%) infested, and lowest among *Mus*, with 26 of 720 (3.6%) infested. Nematodes occurred in 116 of 615 (18.7%) *R. exulans* and 13 of 88 (14.8%) *R. norvegicus*. Nematodes of the genus *Protospirura* were identified from all four species of rodents and a specimen of *Physaloptera* was found in *R. rattus*.

TABLE 4
STOMACH CONTENTS OF RODENTS ASSOCIATED WITH HUMAN HABITATION

FOOD ITEMS	<i>Rattus rattus</i> NO. EXAMINED: 121			<i>Rattus norvegicus</i> NO. EXAMINED: 49		
	FREQUENCIES		VOL. %	FREQUENCIES		VOL. %
	NO.	%		NO.	%	
Fruits and berries	22	18.2	10.7	4	8.2	5.2
Grass (seeds)	11	9.1	6.0	5	10.2	7.4
Grass (stalks)	29	24.0	20.9	3	6.1	5.3
Insects	10*	8.3	2.9	1	2.0	0.1
Sugar cane	15	12.4	11.1	5	10.2	7.7
Nuts	8	6.6	5.8	3	6.1	5.9
Unidentified materials	49	40.5	40.2	27	55.1	60.1
Animal flesh	5	4.1	2.3	6	12.2	5.7
Earthworms				1	2.0	0.1
Corn				1	2.0	2.4

* Includes adults, larvae and egg masses.

DISCUSSION AND CONCLUSIONS

Caum (1922) found that sugar cane by itself was an inadequate diet for rats, for those he had kept on a strict cane diet showed symptoms of malnutrition and partial starvation. Yet in the Hamakua study sugar cane was the preferred food of *R. exulans* in cane fields as well as in gulches and of *R. rattus* in cane fields. *R. rattus* in gulches did not display this strong attraction toward sugar cane, presumably because other preferred foods were more easily available.

A study of rats inhabiting gulches adjacent to cane fields on the Island of Kauai (Spencer, 1938) showed results similar to mine: sugar cane comprised 26% of the food materials of the gulch-inhabiting *R. exulans*, but was absent from the diet of *R. rattus* in the same habitat.

Caum (1922) hypothesized that rats feed on sugar cane only incidentally or in order to expose and feed upon the caneborers infesting the stalks. These hypotheses seem very unlikely, however, as the data showed that too many rats were attracted to sugar cane and consumed too much of it for it to be an incidental food item; moreover very few insects of any kind were found with the ingested sugar cane.

Doty (1945) stated, "the availability of protein foods is the limiting factor controlling the increase of rats in cane fields and adjacent waste areas." Protein foods such as insects, lower invertebrates, and animal flesh were available, with insects forming a large part of the diet of *Mus* in the selected cane fields. Rats in the same habitat did not utilize these sources of protein as much as did *Mus* but, instead, fed heavily on grass stalks, which are also a source of crude protein. Hosaka (1957) reported average crude protein (green weight basis) of *Panicum maximum* as 1.2% and of *P. purpurascens* as 1.8%. My findings indicate that the various rodents tend to satisfy their nutritional requirements in different ways.

In cane fields rodent populations are not necessarily limited only by the availability of protein foods, but also by other environmental conditions, and perhaps by behavioral and physiological traits as well. The diets, and hence the prosperity, of rats depend, therefore, largely upon the materials available to them, which in turn may influence their choice of habitat, and upon their abilities to exploit these materials.

In cane fields *Mus* and *R. exulans* were the predominant species and *R. rattus* was present in small numbers, but only a single *R. norvegicus* was found. In gulches *R. exulans* and *R. rattus* were the prominent species. In areas of human habitation only *R. rattus* and *R. norvegicus* were examined, primarily to augment inadequate samples from the other habitats. *R. rattus* thrived in gardens and orchards, but *R. norvegicus* was abundant only near houses, live-stock pens, poultry coops, or slaughter houses. These differences in the species composition of rodents within each of the three habitats may reflect differences in utility, preference, or availability of food sources as well as in selection of cover. Eskey (1934) captured 56% *R. rattus*, 36% *R. norvegicus*, and 8% *R. exulans* inside and within 50 ft of buildings; 64% *R. rattus*, 16% *R. norvegicus*, and 20% *R. exulans* were caught 51–500 ft from buildings; and 72% *R. rattus*, 9% *R. norvegicus*, and 19% *R. exulans* were trapped more than 500 ft from buildings.

Spencer (1938) found that *R. rattus* preferred wild foods and *R. norvegicus* domestic foods, and that *R. exulans* was intermediate in preference between wild and domestic foods, but inclined toward domestic foods. However, the present findings show that *R. exulans* prefers wild foods; *R. rattus* uses both wild and domestic types, but is inclined toward wild foods, and *R. norvegicus* prefers domestic foods. Calhoun (1962) found that Norway rats took garbage more readily than the commercially prepared food left in feed troughs of penned rats, showing prominent selection between kinds of domestic foods. These findings indicate that while *R. rattus* can easily adapt itself to most habitats, *R. norvegicus* in particular and *R. exulans* to a lesser degree are rather limited in their use of habitats and food sources. Schein and Orgain (1953) found that rats generally preferred foods that promoted gain in body weight and avoided foods not useful to them. Under present conditions in the Hamakua district, the most versatile of the three species of rats appears to be *R. rattus*, which utilizes a wide variety of domestic and wild food sources and adapts itself readily to field habitats as well as to domestic environments. *R. exulans*, however, is restricted to field and gulch environments and depends wholly on

LIST OF IDENTIFIED PLANTS USED BY RODENTS AS FOOD

PLANT	PARTS EATEN
GRAMINEAE	
<i>Paspalum conjugatum</i> (Hilo grass)	stalks and seeds
<i>Setaria palmifolia</i> (palm grass)	stalks and seeds
<i>Panicum maximum</i> (Guinea grass)	stalks and seeds
<i>Panicum purpurascens</i> (para grass)	stalks and seeds
<i>Dignaria henryi</i> (Henry crabgrass)	seeds
<i>Saccharum officinarum</i> (sugar cane)	internodes
CYPERACEAE	
<i>Kyllinga pumila</i> (sedge)	seeds
LEGUMINOSAE	
<i>Desmodium</i> sp. (beggar weed)	pea pods
COMMELINACEAE	
<i>Commelina nudiflora</i> (honobono)	stem
COMPOSITAE	
<i>Emilia flammea</i> (Flora's paint brush)	seeds
MYRTACEAE	
<i>Psidium guajava</i> (guava)	seeds and fleshy pulp
<i>Eugenia cumini</i> (Java plum)	fleshy pulp
PASSIFLORACEAE	
<i>Passiflora</i> sp. (Passion fruit)	seeds
SOLANACEAE	
<i>Physalis peruviana</i> (poha)	whole berry
<i>Solanum nigrum</i> (night shade or popolo berry)	whole berry
ROSACEAE	
<i>Rubus rosaefolius</i> (thimble berry)	whole berry
EUPHORBIACEAE	
<i>Aleurites moluccana</i> (kukui nut)	nut

the food sources available in these habitats. This dependence on wild foods has developed this rat into an efficient feeder on grass seeds and stalks, sugar cane, and a wide variety of other wild foods. The scarcity of Norway rats in the fields and gulches may be simply because their adaptation to survival in the wild has become impaired. This may mean that they are no longer able to utilize successfully a diet that is relatively poor in protein because of changes in ability to select foods, changes in quality of foods available, or changes in internal physiology.

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Preliminary Soil Mineralogy Studies on Krasnozems in the Innisfail District of North Queensland, Australia

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ABSTRACT: A preliminary investigation of four soil series of the Pin Gin family of krasnozem soils has confirmed the results of field observation on their history and has pointed to the diverse nature of their origins and weathering processes. The weathering pattern and origin can account for differences in their fertility in the virgin state.

STUDIES OF THE MINERALOGY of soils can lead to a better understanding of the origin and history of soils and to predicting their physical and chemical behaviour as a medium for the growth of plants. Sherman (1955:110) has discussed this aspect in relation to krasnozems in Hawaii. With this in mind the author, in 1962, commenced an investigation of soils in the sugar cane growing area of Goondi near Innisfail, Queensland. Soils were classified and mapped, and samples were taken from modal profiles for further study.

This paper describes the investigations carried out on the Pin Gin family of soils which are classified as krasnozems (Stevens, 1953: 24-26), latosols (Cline, 1955:70), or oxisols (soil survey staff, U.S.D.A. 1960:238-247). Other workers have examined the mineralogy of North Queensland soils. Leverington (1955: 9) reported on several alluvial samples near the Goondi area. Simonett (1961) and Simonett and Bauleke (1963) related rainfall to the weathering mean in a detailed study of several krasnozem profiles in the Cairns-Atherton region. Robinson (1964) has studied samples collected by Teakle (1950) on the Atherton Tableland. He established that there was a relationship between mean annual rainfall and the presence of gibbsite. The work both of Simonett and of Robinson confirmed that of Tanada (1951) in Hawaii, who showed a similar relationship of weathering stage to mean annual rainfall.

SOIL DESCRIPTIONS

The soils are developed in an area of approximately 140 inches rainfall per annum. There is a distinct dry season from May to December.

The Pin Gin family has been classified into four soil series on the basis of texture as determined in the field, the occurrence of gravels, and the presence of euhedral quartz. Tentative conclusions on the origin of these soils were drawn from field observations.

Pin Gin Series (Darveniza Farm)

0-7 inches. Yellow-red (dry) 5YR 4/6, dusky-red (moist) 10R 3/4 loam. Moderate fine granular structure. Friable when moist, slightly hard when dry.

7-48+ inches. Yellow-red (dry) 5YR 4/6, dusky-red (moist) 10R 3/4 loam. Gradually developing to fragmental structure which is friable when moist. Infrequent fine clear quartz at depth with occasional gravel.

This soil generally grades into weathered olivine basalt at lower depths. The basalt originates from several vents on the eastern and western edges of the Johnstone River Valley which were formed in recent times, after the main tableland eruptions.

Eubenangee Series (O'Connor Farm)

0-8 inches. Yellow-red (dry) 5YR 4/6, dark red-brown (moist) 2.5YR 3/4 loam. Weak fine subangular blocky structure with friable to firm consistence. Infrequent gravel.

8-33 inches. Dusky-red (moist) 10R 3/3 loam. Weak fine granular structure with firm to friable consistence, gravel common.

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33–36 inches. As above with gravelly “stone” line consisting of “cuirasse.”

36 inches. Similar to 8–33 inch layer.

The soil contains an amount of clear euhedral quartz with some stone lines of basaltic and nonbasaltic origin, and occurs generally over steep hills. Field observations, therefore, seemed to indicate that the soil was of mixed origin, containing colluvial materials derived from basaltic and nonbasaltic sources.

Daradgee Series (McAvoy Farm)

0–8 inches. Yellow-red (dry) 5YR 4/8, dark red-brown (moist) 2.5YR 3/4 clay loam. Moderate fine granular structure. Friable consistence when moist.

8–44+ inches. Dusky-red (moist) 10R 3/4 grading to dark red (moist) 10R 3/6 clay loam. Fragmental, firm consistence when moist.

This soil appears at elevations of approximately 50–80 ft above sea level and is associated with upper-level river terraces. In some areas it occurs as a band of uniform width between the river terraces and Pin Gin or Eubenangee soils. These field observations seemed to indicate that the soil had an alluvial origin.

Mundoo Series (Grima Farm)

0–8 inches. Yellow-red (dry) 5YR 4/6, dark red-brown (moist) 2.5YR 3/4 loam. Apedal, friable with some gravel plentiful, fine, euhedral, clear quartz.

8–30 inches. Dark red (moist) 10R 3/6, gravelly loam. Fragmental, firm consistence when moist, some gravel and plentiful fine, euhedral clear quartz.

30–42 inches. Similar to 8–30 inch layer, but plentiful gravel.

42+ inches. Similar to 8–30 inch layer.

The main features of the Mundoo series are the abundance of clear quartz throughout the profile and the occurrence of scattered, discontinuous “cuirasse” layers. The soil forms a gently sloping dissected plain and can be traced under the olivine basalt flow. It could be hypothesised from field observations that this soil was of nonbasaltic origin which had undergone a laterization process, had been covered by a basalt flow, and later was exposed.

Crook and McGarity (1955) have described

the presence of considerable quantities of clear, high-temperature, euhedral quartz in some krasnozems soils of the Lismore area. They concluded that the quartz was derived from rhyolitic tuffs. In the case of the Mundoo soil, quartz could be derived from quartz rhyolite of the Upper Paleozoic Glen Gordon volcanics. However, as the nearest outcrop is 26 miles to the southwest, it is difficult to attribute the origin of quartz to this source, even though there is no other satisfactory explanation.

LABORATORY METHODS

Soil samples from pit profiles were air dried and passed through a 2-mm sieve. Air drying was used because field moisture contents were in the order of 25–40% by weight and indicated that allophane was not present.

After treatment with H_2O_2 , “free” iron was extracted, using the dithionite method (Jackson, 1956:57). The clay ($< 2\mu$) fraction was separated by centrifugation and the silt and sand fractions by sieving. X-ray diffraction patterns were obtained on oriented clay samples which were washed to remove excess salts. The heavy and light mineral fractions were separated by flotation in bromoform, using the silt size samples. These fractions were dried and weighed separately, then mounted in Canada balsam for microscopic investigations. The percentage of tourmaline and zircon was estimated by counting mineral grains in the heavy fraction. Differential thermal analysis was carried out on air-dried samples ground to pass through a 70-mesh sieve, using 0.4-gm samples with a heating rate of approximately 10 C per minute. Samples were treated with hot 0.5N sodium hydroxide and were analysed again on the DTA apparatus to distinguish the goethite from the gibbsite peak.

RESULTS AND DISCUSSION

The table shows marked differences in mineralogical properties among the four soil series.

Light/Heavy Mineral Ratio

Because most of the light fraction is quartz and the heavy fraction is magnetite the light/

TABLE 1
SOIL MINERALOGY DATA ON THE PIN GIN FAMILY OF KRASNOZEMS

SOIL AND LOCATION	DEPTH INCHES	% FREE IRON	SILT FRACTION			X-RAY DATA				DTA DATA		
			L/H* RATIO	% TOURMALINE	% ZIRCON	KAOLIN	GIBBSITE	HEMATITE	KAOLIN	GIBBSITE	GOETHITE	
Pin Gin loam (Jones farm)	0-2	11.2	.47									
	4-6	10.6										
	9-11	11.0		nil		M.S.†	M.S.	M.W.	M.S.	M.S.	M	
	16-18	11.2										
	22-24	11.5		nil	nil	M.S.	M.S.	M.W.	M.S.	M.S.	M	
Eubenangee clay loam (Blundell farm)	1-3	18.5}	.3	.5	1.1	M	S	S	M	S	M	
	4-6	16.9}										
	9-11	16.8										
	12-14	16.9}			1.0	M	S	S	M	S	M	
	15-17	16.5}										
Daradgee clay loam (McAvoy farm)	3-5	7.7	14.2	1.5	1.5	M.S.	M	M.W.	S	M	M.W.	
	7-9	7.7		—	—							
	11-13	7.6		2.1	1.1							
	13-15	8.1		3.7	2.3	M.S.	M	M.W.	S	M	M.W.	
	20-22	8.3		3.4	4.1							
Mundoo clay loam (Foniatti farm)	0-7	6.8	19.2	3.9	7.9	V.W.	V.S.	M.W.	V.W.	V.S.	M.W.	
	7-13	7.8		—	—							
	13-19	5.1		13.1	4.2	V.W.	V.S.	M.W.	V.W.	V.S.	M.W.	
	19-25	4.2		26.7	2.2	17.2						

* L/H refers to the ratio of the light to the heavy fraction in the silt fraction.

† Intensity of peaks indicated as follows: V.S., very strong; S, strong; M, medium; M.W., medium weak; W, weak.

heavy mineral ratio is often a guide to the origin of the soil material. A low ratio reflects a basic rock origin, and a high ratio an acidic rock origin (Carroll, 1949:23). However, it could indicate a certain weathering stage (Jackson and Sherman, 1953:239), since a low ratio may represent a highly weathered soil of either basic or acidic rock origin.

Zircon and Tourmaline

The presence of zircon and tourmaline shows that some of the soil material is of acid and intermediate igneous rock origin (Milner, 1940:355). These minerals can survive several erosion cycles and are accompanied in these soils by minerals (magnetite, quartz) which can also survive several cycles. It is most likely, therefore, that the Daradgee and Mundoo soils are derived from reworked sediments. The Eubenangee soils show some evidence of this, but the Pin Gin soils do not.

X-Ray and D.T.A. Data

These data show differences in kaolin and gibbsite content from the gibbsite-dominant Mundoo soil to the kaolin-dominant Daradgee soil. According to Jackson and Sherman (1953:239), the classification of these soils into their order of weathering based on kaolin, gibbsite, and goethite content would be: Mundoo soils (most weathered), Eubenangee soils, Pin Gin soils, Daradgee soils (least weathered).

"Free" Iron

The free iron content shows the Eubenangee soil to be highly weathered and, because of the relatively low figures for a well weathered soil, appears to confirm the impression that the Mundoo soil is not of basic rock origin.

Field Observation and Mineralogy Studies

The field observations (given under soil descriptions) are largely confirmed by the mineralogy studies.

The Pin Gin soil is derived primarily from the basaltic material in the lower profile, and, while it is of recent origin, has weathered rapidly to produce some gibbsite and goethite. The parent material of the Eubenangee soil is largely basalt. However, the presence of zircon

and tourmaline shows that some material is of acid rock origin. Therefore, it is colluvial material from mixed sources which (according to the gibbsite, goethite and free iron content) has been highly weathered or has derived from highly weathered sources. The Daradgee soil shows ample evidence that the material has been reworked and is partly of nonbasaltic origin. The weathering stage is not advanced. Similarly, the Mundoo soil consists of reworked sediments (shown by the high tourmaline and zircon contents), but, inasmuch as it contains a large proportion of gibbsite, it is highly weathered. From the presence of this soil beneath post-Tertiary flows and the occurrence of a general laterisation period in the Pliocene (Connah and Hubble, 1960), it is assumed that most of the weathering process took place in the Pliocene. The soil remained buried by basalt flows until recent times.

It is of interest, then, that these four soil series, classed generally as krasnozems or lateritic krasnozems, have different origins and have undergone different weathering processes.

Fertility Status and Weathering

Much has been written about the correlation of soil classes with fertility status and crop or pasture production (Butler, 1964). The general conclusion appears to be that there is little correlation between series and that the variation from series to series is as high as that within the series. This is especially so in sugar cane growing regions which have been growing cane for up to 50 years (Monteith, 1949). In this case, however, the soil type can be related to production in the initial establishment period. The Mundoo soil was abandoned for cane growing at one stage and has been brought back into production only by the use of factory filter waste, molasses, and great amounts of fertilizer. The soil has been the most infertile of the four in the Pin Gin family. The establishment of cane growing was difficult on the Eubenangee soils also, but growth responded well to factory filter waste and superphosphate. The Pin Gin and Daradgee soils have not proved to be difficult soils for cane growing. The order of fertility in the early period of cane growing is, in this case, similar to the order of weathering. Therefore, a mineralogical appraisal of virgin

soils should be a guide to production performance.

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NOTES

Adventitious Roots of *Eucalyptus robusta* in Hawaii

RONALD M. LANNER¹

ADVENTITIOUS ROOTING on the trunks and limbs of *Eucalyptus robusta* Sm., a species widely planted in Hawaii, is a remarkable example of how a new environment can change a plant's growth habit. *E. robusta* is native to swampy areas on the coast of southeastern Australia, where annual rainfall ranges from 40 to 60 inches (Forestry and Timber Bureau, 1957). Layering of prostrate stems sometimes occurs there, but adventitious roots on standing trees seem to be unknown.²

ORIGIN AND GROWTH OF THE ROOTS

Newly initiated roots may grow through the thick fibrous bark into the open air, or they may grow downward while remaining within the bark. LeBarron (1962:18) reported that these roots can extend to the ground separate from the trunk. In all cases I have observed, roots that grew into the open died back when only a few inches long. I tried to trace several of these roots by dissecting trunk sections at the point where a root appears, but in all cases the root traces disappeared at a point outside of the trunk pith.

Typically, the young roots remain inside the bark, branching freely. Eventually they enter the soil at the base of the tree without having had their growing points exposed to the air, except for brief periods when they grew out of a ridge of bark, across a fissure, and into an adjacent ridge.

Growing roots thicken and eventually burst through the bark. This process, aided by gradual sloughing of the outer bark, places the adventitious roots outside the trunk (Fig. 1), but by

then the roots are protected from dessication by their own bark. In extreme cases, large roots may completely conceal the trunk.

OCCURRENCE OF ADVENTITIOUS ROOTS

Stands in which trees commonly bear adventitious roots are generally in wet climates. Thus, these roots are common in Hilo, Piihonua, and Mountain View, where median annual rainfall is 147, 210, and 195 inches, respectively (Taliaferro, 1959), and comparatively uncommon at Waikii, Honokaa, and Laupahoehoe (m. a. r. 23, 88, and 100 inches, respectively). At Waimea and Puu Kapu (m. a. r. 39 and 48 inches) frequent fogs compensate for low rainfall and permit adventitious roots to persist.

Within a closed stand, large adventitious roots are found mainly on "wolf" trees and border trees. Open-grown trees with massive spreading limbs generally have the largest adventitious roots (Fig. 1). In contrast, small-



FIG. 1. Strongly developed adventitious roots emerging from crotches of open-grown *E. robusta* near Kurtistown, Hawaii.

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² Personal correspondence with M. R. Jacobs, Forestry and Timber Bureau, Canberra, Australia, Sept. 23, 1963.



FIG. 2. Trunks of small-crowned trees in closed stands, normally free of persistent adventitious roots. This stand is in Glenwood, Hawaii.

crowned, fine-limbed trees typical of dense forests usually have trunks free of all but the finest roots (Fig. 2).

Persistent adventitious roots generally emerge from the upper trunk, crotches of large limbs, and the underside of large limbs. No large roots have been found emerging from the upper surface of a limb, or from a point low on the unbranched portion of a trunk.

DISCUSSION

Adventitious rooting is controlled by moisture level of the bark. *E. robusta* bark is fibrous, absorbent, and more than 7 inches thick on some large trees. It is an efficient reservoir for

water. In some areas it is almost continuously saturated. Both rainfall and fog drip are effective in maintaining high bark moisture content.

Some parts of a tree receive more water, in the form of stemflow, than others. Stemflow is concentrated in large crotches and on the main stem. Because *E. robusta* bark is absorbent, water drains to the lower surface of a near-horizontal limb as well as down the limb toward its junction with the trunk. The bark on the lower side of the limb may be a more effective reservoir, being about twice as thick as the upper-side bark (e.g., 1/2 vs. 1/4 inch) and less subject to drying during periods of clear weather. Penfound and Mackaness (1940:168) also found distinct "flowways" running down the spreading limbs of live oaks and down the trunks. Most of the live oak stemflow coursed along the upper surface of the limbs, probably because the bark was not highly absorbent.

By examining trees after showers, an observer can discriminate wet and dry zones of the bark by their appearance or by feel. He can see that trees with high small crowns often conduct only enough stemflow to saturate the limbs. But spreading-crowned trees with massive branch systems channel enough stemflow down the trunk to saturate the bark for a considerable distance below the crown. Thus, the location of wet bark is partly governed by crown size and configuration. Inasmuch as these attributes are strongly influenced by spacing, adventitious roots are unlikely to become prominent on trees in closed stands.

A somewhat analogous situation is the layering of woody plants into pads of moist humus accumulated by epiphytes (Herbert, 1958:23). But in *E. robusta* the bark itself is the medium that supplies moisture to the adventitious roots.

E. robusta has been planted in other tropical countries (Penfold and Willis, 1961), and adventitious rooting will probably be encountered wherever moisture conditions are satisfactory. M. R. Jacobs, in a letter to the author in 1963, said that he observed such rooting in Uganda and Argentina. There is also a recent report of adventitious roots of *E. robusta* and *E. camaldulensis* Dehnh. in a greenhouse in Russia, where relative humidity was maintained at 80–90% (Gerasimov, 1962:1531). In Australia, *E. camaldulensis* puts forth adventitious roots

from parts of the lower trunk subject to periodic flooding (Jacobs, 1955:145). But because *E. robusta* does not grow under conditions favorable to root induction, its ability to form such roots is not evident within its natural range.

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An Unusual Bisexual *Agathis* Cone

RONALD M. LANNER¹

BISEXUAL CONES have been observed in many genera of the Coniferae. Normally such a cone consists of a functional male strobilus with several ovulate scales at the distal end. This configuration has been found in *Pinus*, *Picea*, *Pseudotsuga*, *Juniperus*, *Sequoia*, and *Abies* (Jack, 1895; Coulter and Chamberlain, 1910; Littlefield, 1931; Mergen and Koerting, 1957; Mergen, 1963). According to Chamberlain (1935:279), cases have been reported in which the base was female and the tip male, but he cites no examples or references. Perhaps the only published report of such a cone is Pauley's description (1942:62) of a single bisexual strobilus of *Picea glauca* (Moench) Voss.²

A fallen bisexual cone of Queensland kauri (*Agathis brownii* [Lemaire] L. H. Bailey) was found in May, 1964 at the nursery of the Hawaii Forestry Division at Hilo, Hawaii. It was female at the base and male at the tip (Fig. 1). Examination of several thousand other fallen male cones from 25 trees failed to turn up another that was in any way anomalous. Such cones are fairly common, however, on some Queensland kauris growing in Honolulu.³

The genus *Agathis* is native to Australia, New Zealand, New Caledonia, Fiji, the Philippines, and the Malay Peninsula. Dallimore and Jackson (1961:176-177) placed it in the Araucarinae Tribe of the Pinaceae.

Though female at the base, this bisexual cone lacked the persistent stalk of the normal seed cone (Fig. 1). It was cast in the same way as were the normal male strobili. When examined under low magnification, the cone showed ap-

parently normal development of both the ovulate and the staminate scales. Pollen was almost ready to be shed, and many ovules had developed into immature seeds with well-defined wings.

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FIG. 1. Normal and bisexual cones of Queensland kauri compared. Left to right: normal male strobilus just after pollen shedding; bisexual cone; immature female cone. Scale is in inches.

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² An account of similar cones on *Picea smithiana* Boiss. by Santamour (1959) was noticed after submission of this article.

³ Personal correspondence with R. K. LeBarron, Hawaii Forestry Division, Honolulu, Hawaii, June 2, 1964, and examination of his specimens.

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Observations on Copulation in the New Zealand Grapsid Crab *Hemigrapsus crenulatus* (M.Edw.)

JOHN C. YALDWYN¹

KNUDSEN IN THIS JOURNAL (1964a:9, et seq.), and elsewhere (1964b), recently summarized existing knowledge of copulation and sperm transfer in the brachyuran crabs. In brief, he was able to generalize from the few published records that in Cancridae (Xanthidae and Cancridae) there could be elaborate courtship prior to the female moult, copulation occurred while the female was in the soft-shell condition, and the typical position was male-over-female. In grapsid and majid crabs, however, there appeared to be little or no courtship, copulation occurred while the female was in the hard-shell condition (in the only record of the majid *Pugettia producta* the female was even ovigerous), and in contrast to the Cancridae the typical position was female-over-male.

The first record of copulation in the widespread family Grapsidae was that of Hiatt (1948) for the northern Pacific, American, and Asiatic species, *Pachygrapsus crassipes* Randall. Additional details for this species are given by Bovbjerg (1960). He describes a limited amount of precopulatory courtship as an extension to Hiatt's data. The only other records in this family appear to be those of Knudsen (1964a) for the North American West Coast species *Hemigrapsus nudus* (Dana) and *H. oregonensis* (Dana). Following Knudsen's plea (1964b:41) for further detailed observations on brachyuran copulation, these notes on the New Zealand species, *Hemigrapsus crenulatus* (H. Milne Edwards), are presented as a partial description of mating in this southern shore crab.

H. crenulatus is a common, medium-sized grapsid of intertidal mud flats and similar protected environments in New Zealand (see Bennett, 1964:81 and Dell, 1963:54), and also occurs in similar habitats in southern Chile (Garth, 1957:97). The following notes were

made by the author during field work in 1954 on the extensive intertidal flats to the east of the Hutt River mouth, Wellington Harbour, in an area now completely "reclaimed" and developed for industrial building.

On 11 September 1954, *Hemigrapsus crenulatus* was found to be common under pieces of wood and among algae and shells on intertidal flats at the mouth of the Hutt River. Several specimens, including ovigerous females, were brought to the laboratory for observation. After being confined together in a collecting jar for some hours, two specimens were seen to be in copulation. The jar was dry, as the water they had been in for some time had just been discarded.

The female was slightly smaller than the male, and ventral surface was placed to ventral surface. The female was slightly more posterior than the male. The latter enclosed the female within its walking legs, which were right around those of the female and on to the dorsal surface of her carapace. The female's legs were stretched out laterally, not attempting to grip the male. The male's chelipeds were held out aggressively over the anterior part of the carapace of the female. The latter's chelipeds were folded under her. The female abdomen was opened right back and the extreme end was hooked on to the posterior edge of the male carapace. When I looked between them, the male abdomen appeared to be opened out, as I could see an open groove. (I did not observe the position of the pleopods.) The mouthparts of the male were working rapidly. The pair remained as described for about 10 minutes; they could move whichever way up they were, and they were considerably disturbed by the other crabs in the container. When the pair broke apart the male took up an aggressive stance, lying over the dorsal surface of the female.

The behaviour described above supports as far as possible Knudsen's generalizations for

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Manuscript received February 19, 1965.

the Grapsidae; no courtship was observed, the female was in the hard-shell condition, and it appears that, at least some of the time, the position was female-over-male. This latter point, however, is not specifically covered in the notes, the only record now of these observations, although the remark "they could move whichever way up they were" implies that both positions were seen. This was probably due to the disturbed nature of the relationship. We can assume that the female was not ovigerous, because if she had been this extraordinary fact would have been clearly visible under the folded-back abdomen.

Allowing for the incomplete nature of these observations, copulation has now been recorded in the Grapsidae for three species of the genus *Hemigrapsus* and one of *Pachygrapsus*, all from the Pacific area.

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Siphonosoma hawaiiense, a New Sipunculoid from Hawaii (Sipunculoidea)

S. J. EDMONDS¹

Siphonosoma hawaiiense n. sp.
Figs. 1–4

Siphonosoma Spengel, 1912; Fisher, 1950
p. 805; Fisher, 1952 p. 380.

SPECIMENS AND LOCALITY: Six specimens collected by F. I. Kamemoto on Sept. 29, 1964, from hard-packed sand above the level of low water near Kualoa, Oahu, Hawaii were kindly sent to me for identification by L. G. Eldredge, Department of Zoology, University of Hawaii, Honolulu. A type specimen has been lodged at the Bernice P. Bishop Museum at Honolulu (BM numbers: Invertebrate W-294 for the type specimen, and Invertebrate W-295 for the cotypes).

DESCRIPTION: The length of the trunk is 9–15 cm and the width, which is variable in different parts of any of the specimens, is 3–5 cm. The length of the fully extended introvert of two specimens is 4–5 cm and the width about 2 mm. The colour of the specimens preserved in alcohol is pale straw. The skin of some of the specimens is very thin and almost transparent; of others it is much wrinkled. At the anterior extremity of the introvert of one specimen there is a crown of about 50 short and fine tentacles. The anterior region of the introvert also bears about 30 rows of yellow-coloured, blunt spines the shape of which resembles to some extent that of a slipper. The hooks are about 0.15–0.3 mm long and they become progressively smaller the more posterior they are placed on the introvert. The introvert also bears numerous rings of small yellowish papillae which in the anterior region are closely associated with the hooks. These papillae are about 0.03–0.05 mm in diameter. In the centre of each papilla there is a clear circular area which is surrounded by a yellowish granular region. The papillae on the trunk are of two

kinds: one is small (about 0.03–0.05 mm in diameter) and looks very much like those on the introvert, while the other is larger (0.25–0.40 mm in diameter) but less numerous. The latter kind of papilla is largest at the base of the introvert and on the posterior surface of the trunk.

The longitudinal musculature is not very noticeable externally. When a specimen is dissected, however, 14–17 well-developed longitudinal bands of muscles, which anastomose to some extent, are observable in the midbody region. The circular musculature is continuous. Four introvert retractors arise at different levels, a dorsal pair more anteriorly from muscles 4–5 on each side of the nerve cord and a ventral pair more posteriorly from muscles 2–3. The dorsal and ventral retractors on each side fuse anteriorly to form a single muscle on each side of the oesophagus.

The alimentary canal consists of an oesophagus, descending and ascending intestinal spirals, a short rectum, and an anus. It was filled with coarse particles of sand and coral (?) fragments. An intestinal caecum is present. A polian or contractile vessel with wrinkled edges runs along the dorsal surface of the oesophagus. Strongly developed wing muscles are attached to the posterior part of the rectum. A well-developed spindle muscle is fastened anteriorly to the body-wall in front of the anus and posteriorly at the terminal tip. The spindle muscle gives off anteriorly two strong, wing-like strands of muscle which are fastened to the body-wall along muscle 5 or 6 on each side of the nerve cord near the dorsal retractors. An additional fastener arises from the last whorl of the intestine and runs to the body-wall at a point near the base of the right dorsal retractor. Two fine fasteners also run in an almost parallel manner from the last whorl of the intestine to muscle 1 on each side of the nerve cord at points just posterior to the level of attachment

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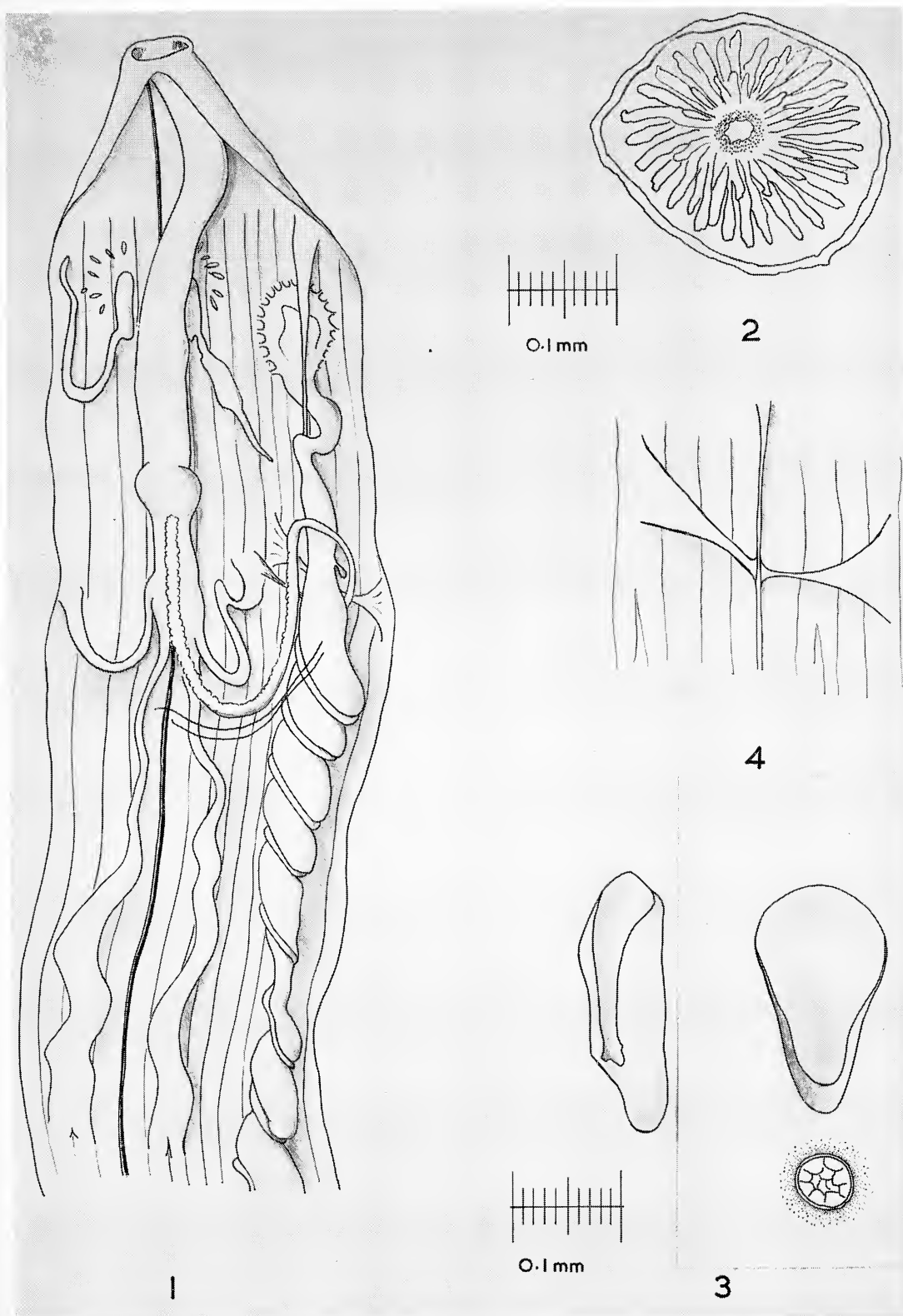


FIG. 1-4. *Siphonosoma hawaiiense*. 1, Dissected specimen; 2, papilla from base of introvert; 3, hooks and papilla from introvert; 4, arrangement of fasteners at anterior extremity of spindle muscle.

of the dorsal retractors. Coelomic papillae but no transverse body dissepiments are present.

The nephridia are large, brown, and free except for about a quarter of their length. They extend as far as the base of the dorsal retractor. Well-developed eggs were found in the body cavities of the two specimens; they were generally uniform in size and about 95–110 μ in diameter. They appeared to be mature. The nerve cord is not fixed firmly to the body-wall.

SYSTEMATIC POSITION: These specimens are members of the subgenus *Siphonosoma sensu strictu* of Fisher 1952. They are very close to *S. pescadolense* Sato 1939 and *S. takatsukii* Sato 1935, the former collected from Formosa and the latter from the Caroline Islands. They differ most noticeably from Sato's species in that they possess a well-developed intestinal or rectal caecum.

I am indebted to Rod. Wells for the drawings of *S. hawaiiense*.

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PACIFIC SCIENCE

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Gill Arches of Teleostean Fishes of the Order Anguilliformes^{1,2}

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THE GILL ARCHES of eels have required a broad, comparative study since Cope (1871) erected a separate order for the morays chiefly on the basis of their highly specialized gill arch skeleton. The work reported herein was undertaken to provide such a study, with the hope that it might contribute to the solution of some of the problems in eel systematics.

SOURCES OF MATERIAL AND ACKNOWLEDGMENTS

Much of the study material, present in the collections of the Department of Zoology, University of Hawaii, was originally obtained from rotenone poisonings in shallow water around Oahu. Additional material was obtained through the courtesy of the following persons: Dr. H. Asano, Kinki University, Japan; Dr. P. Castle, Victoria University of Wellington, N. Z.; Mr. H. Compton and Mr. E. Simmons, Parks and Wildlife Dept., Rockport, Texas; Dr. W. Frehofer, Stanford University; Mr. R. Jones and Mr. R. Snider, University of Hawaii; Dr. S. Jones, Central Marine Fisheries Research Institute, Mandapam Camp, South India; Dr. K. Matsubara, Kyoto University, Japan; Dr. J. Randall, University of Puerto Rico; Dr. R. Rosenblatt, Scripps Institution of Oceanography; Mr. L. Woods, Chicago Natural History Museum.

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METHODS AND MATERIALS

In general, the gill arches were removed as a unit from a given specimen, stained with alizarin in an aqueous solution of 2% potassium hydroxide, cleaned, and examined under a dissecting microscope. Drawings of the bones were executed freehand or, in some cases, with the aid of retouched photographs.

Specimens, usually young adults, of the following species were available for study:

Congridae: *Anago anago*, *Ariosoma bowersi*, *Conger marginatus*, *Congrina aequorea*, *Japanoconger sivicolus*

Heterocongridae: *Gorgasia punctata*, *Gorgasia* sp.

Derichthyidae: *Derichthys serpentinus*

Nettastomidae: *Metapomomys denticulatus*

Muraenesocidae: *Muraenesox cinereus*, *Oxyconger leptognathus*

Ophichthidae: *Ahlia egmontis*, *Echelus myrus*, *Leptenchelys labialis*, *Muraenichthys cookei*, *M. gymnotus*, *M. laticaudata*, *M. macrop-terus*, *M. schultzei*, *Myrophis punctatus*, *M. uropterus*, *Neenchelys buitendijki*, *Schultzidia johnstonensis*, *Bacanichthys teres*, *Brachysomophis henshawi*, *Caecula platyrhyncha*, *Callechelys melanotaenia*, *Cirrhimuraena macgregori*, *Leiuranus semicinctus*, *Letharchus velifer*, *Machaerenchelys phoenixensis*, *Myrichthys maculosus*, *Mystriophis intertinctus*, *Ophichthus polyophthalmus*, *Phyllophichthus xenodontus*

Synphobranchidae: *Synphobranchus affinis*

Simenichelidae: *Simenichelys parasiticus*

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- Dysommidae: *Dysomma anguillare*
 Anguillidae: *Anguilla rostrata*
 Heterenchelidae: *Heterenchelys biaggii*
 Moringuidae: *Moringua javanica*, *M. macrochir*
 Xenocongridae: *Chilorhinus platyrhynchus*,
Chlopsis bicolor, *Kaupichthys brachychirus*,
K. diodontus
 Dysommidae: *Dysommia rugosa*
 Muraenidae: *Anarchias cantonensis*, *A. leucurus*,
Channomuraena vittata, *Uropterygius fuscoguttatus*,
U. knighti, *U. marmoratus*, *U. supraforatus*,
U. tigrinus, *U. xanthopterus*, *Echidna nebulosa*,
E. polyzona, *E. unicolor*, *Enchelycore nigricans*,
Enchelynassa canina, *Evenchelys macrurus*,
Gymnomuraena zebra, *Gymnothorax eurostus*,
G. javanicus, *G. meleagris*, *G. petelli*, *Muraena helena*,
M. pardalis, *Rabula fuscomaculata*, *Strophidon
 brummeri*
 Serrivomeridae: *Serrivomer sector*
 Nemichthyidae: *Avocettina bowersi*, *Cyema
 atrum*, *Nemichthys scolopaceus*

RESULTS

In all of the eels examined, with only one exception, the following bones of the gill arch skeleton are present: ceratobranchials and epi-branchials 1, 2, 3, 4 and the upper and lower pharyngeal tooth-bearing dermal bones. Pharyngobranchial 1 is absent without known exception. Other bones of the gill arch skeleton, either present or absent, are summarized in Table 1, for the species examined and others reported in the literature. Information on eel gill arches is present in the following papers: Asano (1962); Beebe (1935*a*, 1935*b*); Beebe and Crane (1936, 1937*a*, 1937*b*); Böhlke (1957); Castle (1961); Cope (1871, 1884); Gill (1890*a-e*); Gosline (1950, 1951*a*); Jang (1957); Jaquet (1920); Popta (1904); Regan (1912*b*); Takai (1959); Trewavas (1932).

DISCUSSION

Eel Lineages

Cope (1871, 1884) split the eels into two orders: one, the Coloecephali, included only the morays; the other, the Enchelycephali, included the other eels. Cope apparently did not regard

these two orders as separate lineages. The morays he regarded simply as a specialized offshoot of a more generalized stock, of which the Anguillidae were examples (Cope, 1884: 584).

Cope's two groups were sometimes considered by later authors as orders (e.g., Herre, 1953), as suborders (e.g., Gill, 1890*a*; Jordan and Davis, 1892; Jordan and Evermann, 1896; Jordan and Snyder, 1901), or sometimes as groups without specific rank (e.g., Fowler, 1936).

Regan (1912*b*) did not discuss the matter of eel lineages as such, but in his key to the families he divided the eels into two groups, each including several families, depending on whether the frontal bones are fused or, alternatively, are separated by a suture. Subsequent authors have generally followed Regan, but further suggested that his two groups represent two primary evolutionary lineages within a single order (Gosline, 1951*a*:304-5; Asano, 1962:62).

It is not possible to divide the eels into two such groups on the basis of gill arch characters. Yet Regan's groups seem to this author to be natural ones and his division of the order is used here. It is possible, however, to subdivide one of Regan's groups, that characterized by fused frontal bones, on the basis of gill arch characters discussed below. Thus, in the material comprising this study three lineages are apparent:

1. Anguilloid: Anguillidae, Heterenchelidae, Serrivomeridae, Nemichthyidae(?), Moringuidae, Xenocongridae, Dysommidae, and Muraenidae.
2. Synphobranchoid: Synphobranchidae, Ilyophidae, Simenchelidae, and Dysommidae.
3. Congroid: Congridae, Heterocongridae, Nessorhamphidae, Nettastomidae, Derichthyidae, Ophichthidae, and Muraenesocidae.

During the history of each of these three lineages the gill arch skeleton seems to have been similarly modified. The modifications have involved: (1) progressive enlargement or progressive reduction with eventual loss of certain skeletal parts, (2) simplification in the form of the skeletal parts (loss of grooves and processes), (3) an anterior shift in position of the lower pharyngeal tooth plates, which gradu-

TABLE 1
SUMMARY OF THE GILL ARCHES IN 18 EEL FAMILIES¹

FAMILY AND GENUS	B1	B2	B3	B4	H1	H2	H3	C5	I2	I3	UP3	UP4
Congridae												
<i>Conger</i>	O	O	O	C	O	O	C	O	O	O	O	O
<i>Japanoconger</i>	O	O	O	C	O	O	C	O	O	O	O	O
<i>Anago</i>	O	O	O	C	O	O	C	O	O	O	-O-	
<i>Ariosoma</i>	O	O	O	C	O	O	C	O	O	O	-O-	
<i>Congrina</i>	O	O	O	C	O	O	C	O	O	O	-O-	
Heterocongridae												
<i>Gorgasia</i>	O	O	O	C	O	O	C	O	O	O	-O-	
* <i>Nystaticthys</i>	O	O	O	X	O	O	X	O	O	O	-O-	
Derichthyidae												
<i>Derichthys</i>	O	O	O	C	O	O	C	O	O	O	O	O
Nettastomidae												
<i>Metapomycter</i>	O	O	-	C	O	O	C	O	O	O	O	O
Nessorhamphidae												
* <i>Nessorhamphus</i>	O	O	O	X	O	O	X	?	X	O	O	O
Muraenesocidae												
<i>Oxyconger</i>	O	O	O	C	O	O	C	O	O	O	O	O
<i>Muraenesox</i>	O	O	O	C	O	O	C	O	O	O	-O-	
Synphobranchidae												
<i>Synphobranchus</i>	O	O	O	C	O	O	C	O	R	O	O	O
Simenchelidae												
<i>Simenchelys</i>	O	O	O	C	O	O	C	O	O	O	O	O
Dysommidae												
<i>Dysomma</i>	O	-	-	-	O	O	C	O	-	O	O	O
Ophichthidae												
<i>Echelus</i>	O	C	C	C	O	O	C	O	O	O	O	O
<i>M. punctatus</i>	O	R	-	-	O	O	C	-	O	O	O	O
<i>M. uropterus</i>	O	-	-	-	O	O	C*	-	O	O	O	O
<i>Abliia</i>	O	-	-	-	O	O	-	-	-	O	O	O
<i>Neenchelys</i>	R	-	-	-	O	O	C	-	O	O	O	O
<i>M. laticaudata</i>	-	-	-	-	O	O	C*	-	O	O	O	O
<i>M. cookei</i>	-	-	-	-	O	O	C*	-	C*	O	O	O
<i>M. gymnotus</i>	-	-	-	-	O	O	C*	-	-	O	O	O
<i>M. macropterus</i>	-	-	-	-	O	O	C	-	C*	O	-O-	
<i>M. schultzei</i>	-	-	-	-	O	O	C*	-	-	O	-O-	
<i>Schultzia</i>	-	-	-	-	O	O	C	-	-	O	-O-	
<i>Leptenchelys</i>	-	-	-	-	O	O	-	-	-	O*	-O-	
<i>Ophichthus</i>	O	C	R	R	O	O	C	O*	O	O	O	O
<i>Mystriophis</i>	O	R	R	C	O	O	C	O	O	O	O	O
<i>Brachysomophis</i>	O	C	-	C	O	O	C	O	O	O	O	O
<i>Myrichthys</i>	O	C	R	C	O	O	C	O	O	O	O	O
<i>Bascanichthys</i>	O	C	-	C	O	O	C	O	O	O	O	O
<i>Leiarchus</i>	O	C	-	R	O	O	C	-	O	O	O	O
<i>Cirrhimuraena</i>	O	C	R	R	O	O	C*	C	O	O	O	O
<i>Caecula</i>	O	-	-	C	O	O	C*	O	O	O	O	O
<i>Phyllophichthus</i>	O	R	R	-	O	O	C*	-	O	O	O	O
<i>Callechelys</i>	O	C	-	-	O	O	C	-	O	O	O	O
<i>Leiuranus</i>	O	C	-	C	O	O	C*	-	O	O	-O-	
<i>Machaerenchelys</i>	O	C	-	-	O	O	C*	-	O	O	-O-	

¹ Symbols used: O, ossified; O*, probably ossified and fused with dermal bone; -O-, UP3 and UP4 probably fused together; C, cartilaginous element; C*, cartilaginous process of cerato- or epibranchial; X, cartilaginous or absent; R, rudimentary; -, absent; ?, status unknown. Other symbols as in Figures 1 and 2.

* Not examined in the present study.

TABLE 1 (Continued)

FAMILY AND GENUS	B1	B2	B3	B4	H1	H2	H3	C5	I2	I3	UP3	UP4
Heterenchelidae												
<i>Heterenchelys</i>	O	O	C	C	O	O	C	O	O	O	O	O
Anguillidae												
<i>Anguilla</i>	O	O	—	C	O	O	C	O	O	O	O	O
Serrivomeridae												
<i>Serrivomer</i>	O	C	—	C	O	O	C	O	O	O	O	O
* <i>Platuronides</i>	O	X	X	X	O	O	X	?	O	O	—O—	
Nemichthyidae												
<i>Nemichthys</i>	O	—	—	—	O	O	C*	O	O	O	O	O
<i>Avocettina</i>	C	—	—	—	O	O	C*	O	C*	O	O	O
* <i>Labichthys</i>	X	X	X	X	O	O	X	?	X	O	O	O
* <i>Nematoprora</i>	X	X	X	X	X	X	X	?	?	?	O	O
<i>Cyema</i>	—	—	—	—	C*	C*	C*	—	—	—	—O—	
(Cyema lacks E1, E2, and E3. E4 is ossified.)												
Moringuidae												
<i>M. javanica</i>	C	R	—	—	O	O	C	O	O	O	O	O
<i>M. macrochir</i>	O	—	—	—	O	O	C	O	O	O	O	O
Xenococongriidae												
<i>Cblopsis</i> , etc.	—	—	—	—	O	O	—	O	O	O	O	O
<i>K. diodontus</i>	—	—	—	—	O	O	—	O	R	O	O	O
Dysommidae												
<i>Dysommia</i>	—	—	—	—	O	O	—	O	—	O	—O—	
Muraenidae												
<i>Anarchias</i> , etc.	—	—	—	—	O	O	—	—	—	O*	—O—	
<i>Echidna</i> , etc.	—	—	—	—	—	—	—	—	—	O*	—O—	

ally become supported by the fourth rather than the fifth ceratobranchials.

The tendency toward loss of elements has been so pronounced that it is possible within each lineage to separate primitive from advanced forms simply on the basis of the relative completeness of the gill arch skeleton, the primitive forms having more, the advanced, fewer skeletal elements (Table 1).

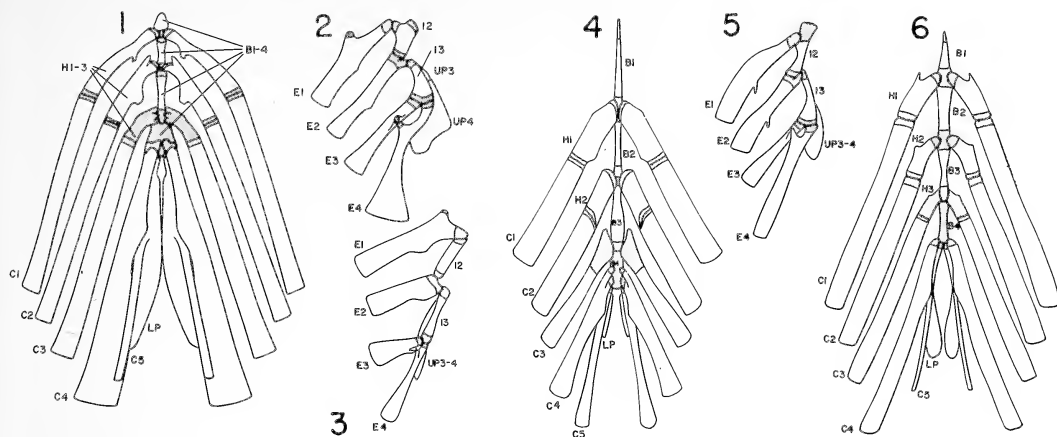
Congroid Lineage

A rather complete set of gill arches is present in most members of this lineage, except for the ophichthids. The arches of *Conger* (Figs. 1, 2) are perhaps the most generalized. Dorsally, epibranchial one (E1) bears an anterior, cartilage-capped process, presumably an articular surface for, or perhaps a rudiment of, pharyngobranchial one, which is not present as an independent skeletal element among eels. Pharyngobranchial two (I2) bears a cartilage-capped medial process, another primitive feature not generally present in eels.

The arches of *Muraenesox* are very similar to those of *Conger*. Those of *Gorgasia* (Figs. 3, 4), *Ariosoma* (Figs. 5, 6), *Japanoconger*, and *Anago* are hardly more specialized.

Most ophichthids are distinguished in having the proximal ends of the dorsal parts of the first and second arches connected through a continuous cartilage, a peculiarity not present in any other of the eel families studied. Among generalized ophichthines might be placed those eels with a reasonably developed series of basi-branchials and an ossified fifth ceratobranchial (C5), namely *Bascanichthys*, *Mystriophis*, *Brachysomophis*, *Ophichthus*, and *Myrichthys*. Even in these forms, however, the basibranchials are somewhat reduced (Table 1), and C5 is in various stages of reduction.

Bascanichthys (Fig. 7) retains one primitive feature not found in the other genera examined, the double articulation of C4 with basibranchial four (B4). In this genus C5 seems reduced to a minute ossicle on the posterior edge of the lower pharyngeal tooth plates.



FIGS. 1-6. 1, *Conger marginatus*, gill arch skeleton, ventral view. B1-4, basibranchials; H1-3, hypobranchials; C1-5, ceratobranchials; LP, lower pharyngeal dermal tooth plates. Cartilage stippled. Articular cartilages at distal tips of ceratobranchials not shown. 2, *Conger marginatus*, dorsal view. E1-4, epibranchials; I2-3, (infra)pharygobranchials; UP3-4, upper pharyngeal dermal tooth plates. Articular cartilages at distal tips of epibranchials not shown. 3 and 4, *Gorgasia* sp. 5 and 6, *Ariosoma bowersi*.

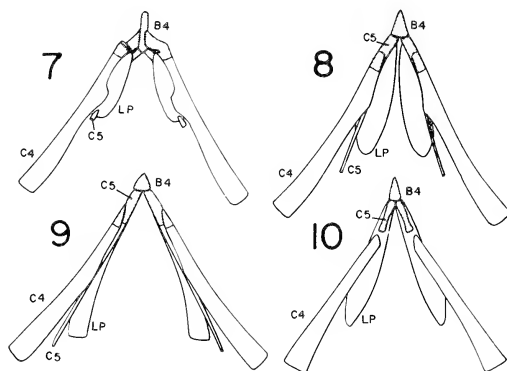
In *Mystriophis* and *Brachysomophis* (Fig. 9) C4 has lost its double articulation with B4, but C5 is prominent. C4, however, is without any direct articulation with B4, being supported entirely by C5, which retains a firm articulation with B4. From this condition may have been derived that of *Myrichthys* (Fig. 8) and *Ophichthus* (Fig. 10). *Cirrhimuraena* and *Myrichthys* are alike in having the proximal portion of C5 cartilaginous, situated between C4 and B4, the distal portion extending posteriorly as a thin filament of cartilage (*Cirrhimuraena*) or bone (*Myrichthys*). In *Letharcus*, C5 is present proximally as a small cartilage between C4 and B4, but seems entirely absent distally. Reduction of C5 has proceeded somewhat differently in *Ophichthus* (Fig. 10). C4 is without a proximal articular cartilage, being supported entirely by the lower pharyngeal tooth plates, which it seems have surrounded and fused with C5, leaving only the intermediate cartilaginous portion of C5 as evidence of the fact.

The only other ophichthine examined having an ossified C5 is *Caecula* (Figs. 11, 20). In this form C4 has retained its primitive connection with B4, but not a double articulation as in *Bascanichthys*.

Gill arch structure in *Phyllophichthus*, *Callechelys*, and *Machaerenchelys* is about that shown

for *Leiuranus* (Figs. 17, 18). C5 is lost altogether, perhaps fused with the tooth plate or with C4.

Relationships between the genera examined here have never been established. Gill arch structures, however, suggest certain relationships. One lineage may perhaps be represented by those forms having C4 not articulating with B4, but being supported by C5, including *Mystriophis*-*Brachysomophis*-*Ophichthus*, with *Myrichthys*, *Cirrhimuraena*-*Letharcus* branch-



FIGS. 7-10. 7, *Bascanichthys teres*, posterior portion of gill arch skeleton, ventral view. Ventral articulation of C4 with B4 not shown on right side, where a portion of cartilage is omitted to show dorsal articulation. 8, *Myrichthys maculosus*. 9, *Brachysomophis hensbawi*. 10, *Ophichthus polyophthalmus*.

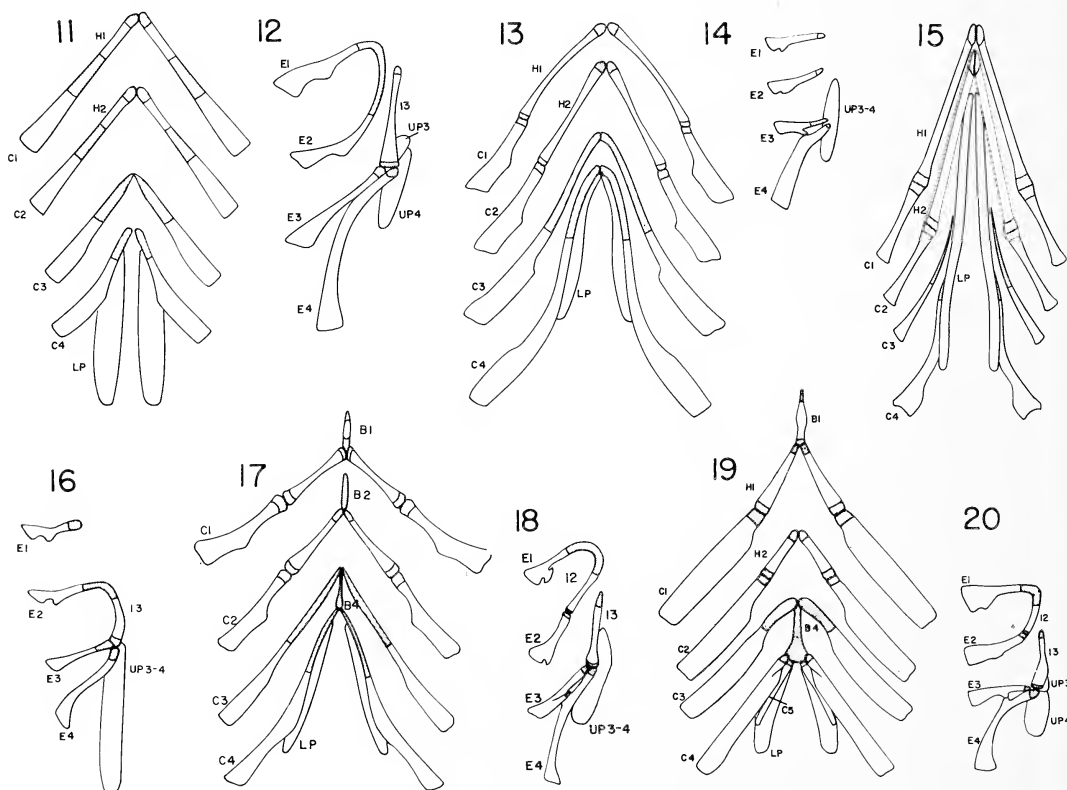
ing off early in its history. Another lineage may be represented by those forms having C4 contacting B4, including *Caecula* and *Bascanichthys*. The remaining genera, *Leiuranus* *Phyllophichthus*, *Machaerenchelys*, and *Callechelys* are generally similar and have no trace of C5. Whether they might be more closely related to one or the other of the groups suggested above cannot therefore be commented on.

Among most members of the subfamily Echelinae the gill arch skeleton is severely reduced and approaches the form characterizing the muraenids. *Echelus*, however, is a notable exception, for its gill arch skeleton is perhaps the most generalized of any of the ophichthids examined (Table 1).

Among echeline eels there is a tendency for the lower pharyngeal tooth plates to be somewhat anteriorly displaced in the more specialized forms. In *Echelus* they occupy a position similar to that of the tooth plates of *Conger*

and are supported by C5. *Schultzidia* (Figs. 11, 16) has the tooth plates posterior in position, supported by C4. *Muraenichthys cookei* (Figs. 12, 13) has them more forward and *M. laticaudata* still more so. In *Ablia* and *Leptenchelys* (Figs. 14, 15) the tooth plates are very elongate, far forward in position, separating the ventral parts of the third arch on either side. In their high degree of specialization *Ablia* and *Leptenchelys* bear some resemblance to the group characterized by *Uropterygius* of the Muraenidae (Table 1, Fig. 41).

There has been continuing discussion of intergeneric relationships between echeline eels, much of which has concerned the limits of the genera *Myrophis* and *Muraenichthys* (Parr, 1930; Myers and Storey, 1939; Myers and Wade, 1941; Wade, 1946; Schultz and Woods, 1949; Gosline, 1950, 1951a, 1951b; Schultz, 1953; Böhlke, 1956, 1960; Nelson, 1966). On the basis of gill arch characters the relationships



FIGS. 11-20. 11, 16, *Schultzidia johnstonensis*. 12 and 13, *Muraenichthys cookei*. 14 and 15, *Leptenchelys labialis*. 17 and 18, *Leiuranus semicinctus*. 19 and 20, *Caecula platyrhyncha*.

between the species examined may be depicted by the rather linear reduction in gill arch elements (Table 1), with *Echelus* being the most primitive form and *Leptenchelys* the most advanced. In view of the variability exhibited in gill arch structure, a supplementary study was made on the sensory canal pores of the following material, mainly from the University of Hawaii collections:

Ablia egmontis, 2 specimens, 103, 235 mm, Puerto Rico; *Myrophis punctatus*, 3, 127–139 mm, Texas Coast; *M. uropterus*, 1, 82 mm, Palmyra; *Muraenichthys cookei*, 1 Oahu, 4 Johnston, 128–225 mm; *M. macropterus*, 1 Hull, 3 Makatea, 102–200 mm; *M. gymnotus*, 1 Aitutaki, 1 Eniwetok, 1 Johnston, 1 Rarotonga, 4 Tahiti, 84–136 mm; *M. laticaudata*, 1 Aitutaki, 1 Bikini, 1 Eniwetok, 2 Onotoa, 1 Rongelap, 2 Tonga, 92–139 mm; *M. schultzei*, 1 Arno, 1 Guadalcanal, 3 Johnston, 1 Papeete, 53–120 mm; *Leptenchelys labialis*, 1 Eniwetok, 5 Johnston, 122–136 mm; *Schultzidia johnstonensis*, 2 Johnston, 1 Midway, 2 Oahu, 84–163 mm.

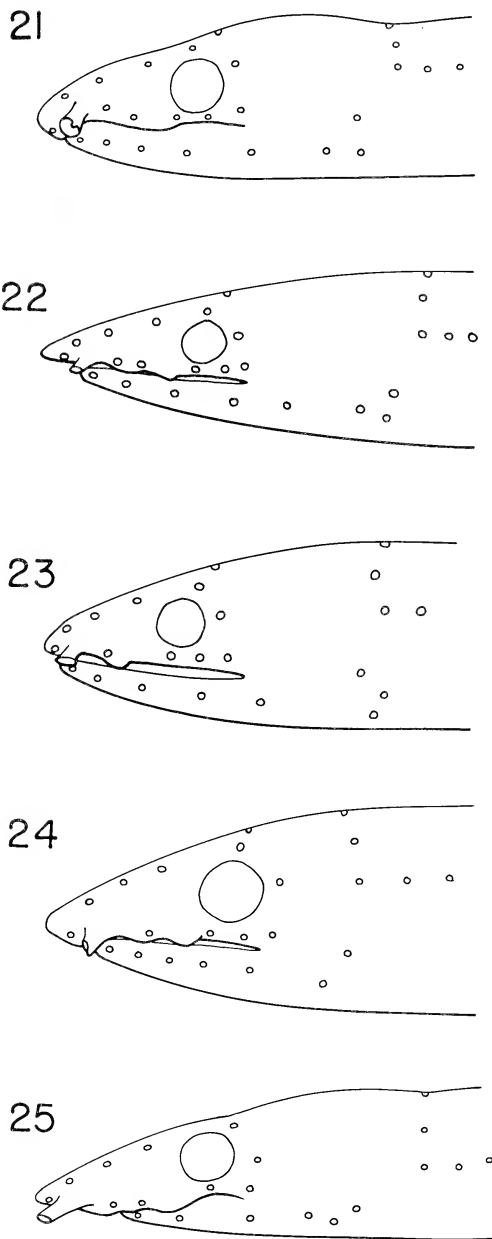
The number and pattern of sensory pores of the head exhibited great stability in specimens of the some species, sometimes being distinctive enough to permit identification on this basis alone.

The pattern of cephalic pores basic to the group is probably that shown in *Myrophis punctatus*, *M. uropterus*, *Ablia egmontis*, *Muraenichthys cookei*, *M. laticaudata*, *M. macropterus* (Fig. 21), and *Pseudomyrophis nimius* (Böhlke, 1960:2–4, fig. 1). The pattern in *Echelus* apparently is secondarily simplified (Allis, 1903; Gosline, 1952), as seems to be that also of *Hesperomyrus* (Myers and Storey, 1939).

The pores of the head are easily divided into groups (paired unless otherwise indicated): a supraorbital group of five pores, beginning with the one on the underside of the snout; a median interorbital pore; a postorbital pore; three pores below the eye; two between the nostrils; five in a row along the lower jaw; three over the preopercle, forming an angle of about 90 degrees; a series of five across the

nape, including the anteriormost pore of the lateral line on either side.

The supraorbital pores, including probably those on the underside of the snout (Allis,



FIGS. 21–25. 21, *Muraenichthys cookei*, sensory pores of the head and anterior trunk. 22, *M. gymnotus*. 23, *M. schultzei*. 24, *Schultzidia johnstonensis*. 25, *Leptenchelys labialis*.

1903), mark the course of the supraorbital canal. The interorbital pore arises from an interorbital commissure by way of a median dorsal opening in the frontal bones. The postorbital pore, those pores below the eye, and those between the nostrils mark the course of the infraorbital canal. Those on the lower jaw and over the preopercle mark the course of the preoperculo-mandibular canal.

M. gymnotus (Fig. 22) is close to the basic pattern, differing only slightly in the position of a few pores. The three below the eye are somewhat posteriorly displaced. The three over the preopercle form an angle perhaps a little less than 90 degrees.

M. schultzei (Fig. 23) diverges more significantly, having the nostrils close together and only a single pore between them. The three pores over the preopercle form an angle considerably greater than 90 degrees.

Schultzidia johnstonensis (Fig. 24) likewise has a single pore between the nostrils. There are but two pores over the preopercle.

Leptenchelys labialis (Fig. 25) has the pore system the most reduced, lacking the median interorbital pore, one of the three below the eye, two of the usual five along the lower jaw. The three over the preopercle form an angle greater than 90 degrees. The pattern of *L. labialis* seems similar to that of *L. pinnaceps* (Schultz, 1953: Fig. 16), but both of these differ markedly from that of *L. vermiformis* (Myers and Wade, 1941: Pl. 10), which has a greater number of pores behind the eye and along the lower jaw. In this regard, it has recently been discovered that the Central Pacific eels described in the genus *Leptenchelys* by Schultz (1953) are probably not congeneric with *Leptenchelys vermiformis* Myers and Wade, the type of the genus (Rosenblatt, personal communication).

Neenchelys buitendijki (Nelson, 1966: Fig. 1A) has only two of the usual three pores over the preopercle. The series along the lower jaw number seven–eight, instead of five. The other pores have the same basic arrangement as in *M. cookei*.

In all the specimens examined the only variability in pore number and position occurred in the pores of the lower jaw. The specimen of *S.*

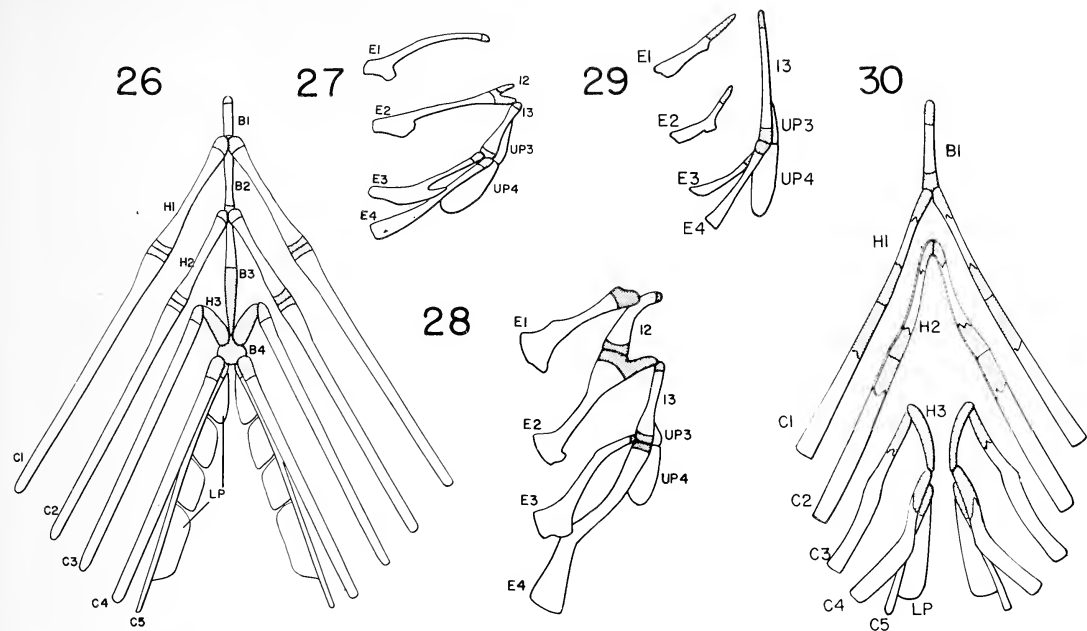
johnstonensis from Johnston Island has six pores on each side. The specimen of *M. laticaudata* from Aitutaki has six on the right side and five on the left.

Ablia, *M. schultzei*, and *Schultzidia* have lateral line pores generally restricted to the trunk, numbering about 40–70. In all other species examined lateral line pores number nearly or over 100 and extend well onto the tail.

The present author agrees with Schultz (1953:61) "that recognition of echelid genera must be done on a world-wide basis and not on the study of local fauna." However, on the basis of this study, *Echelus*, *Myrophis*, *Ablia*, *Muraenichthys*, *Neenchelys*, *Leptenchelys*, and *Schultzidia* might be considered valid genera. *Ablia* seems distinct from *Myrophis* on the basis of gill arch characters. It differs in gill arch structure also from *M. schultzei* and *Schultzidia*, although in all three the dorsal origin is posterior to the anus and lateral line pores are generally absent from the tail. Within the genus *Muraenichthys*, *M. cookei*, *M. laticaudata*, and *M. macropterus* seem quite similar and may be representatives of a generalized stock having given rise to separate offshoots in *M. schultzei* and *M. gymnotus*. *M. schultzei* and *Schultzidia* share some characters as noted above. The specialized jaws and teeth (Gosline, 1951a) and distinctive pharyngeal tooth plates (Figs. 11, 16) of *Schultzidia* would seem to rule out any close relationship with *M. schultzei*. *Leptenchelys* shows no great similarity with any of the other species examined. Its gill arches are perhaps most similar to those of *Ablia*, but the tendency toward forward displacement of the lower pharyngeal tooth plates is also quite pronounced in *M. laticaudata*.

Synphobranchoid Lineage

It is possible to separate *Synphobranchus* (Figs. 26, 27), *Diastobranchus* (Castle, personal communication), *Simenchelys* (Fig. 28; see Jaquet (1920) for ventral view), and *Dysomma* (Figs. 29, 30) from other eels on the basis of the posteriorly directed third hypobranchials. This is in contrast to the condition observed in other eels and bony fishes generally,



FIGS. 26–30. 26 and 27, *Synaphobranchus affinis*. 28, *Simenchelys parasiticus*. 29 and 30, *Dysomma anguillare*.

in which the hypobranchials are characteristically anteriorly directed. The gill skeleton of *Simenchelys* is the most generalized in terms of the number of elements (Table 1), yet that of *Synaphobranchus* has the lower tooth plates in four pairs. Other such multiple tooth plates occur in such lower teleosts as *Osteoglossum*, *Hiodon*, *Elops*, and *Albula*, but not generally in other teleosts nor in the other eels examined. In *Conger*, however, the lower tooth plates are initially in two pairs which later fuse together and with C5 during ontogeny to form a single pair (personal observations). The multiple tooth plates of *Synaphobranchus*, therefore, seem to be primitive features and are evidence against the derivation of *Synaphobranchus* from such a form as *Conger*. For this reason it seems appropriate to consider the synaphobranchoid lineage as possibly equivalent to the other two, the congroid and the anguilloid.

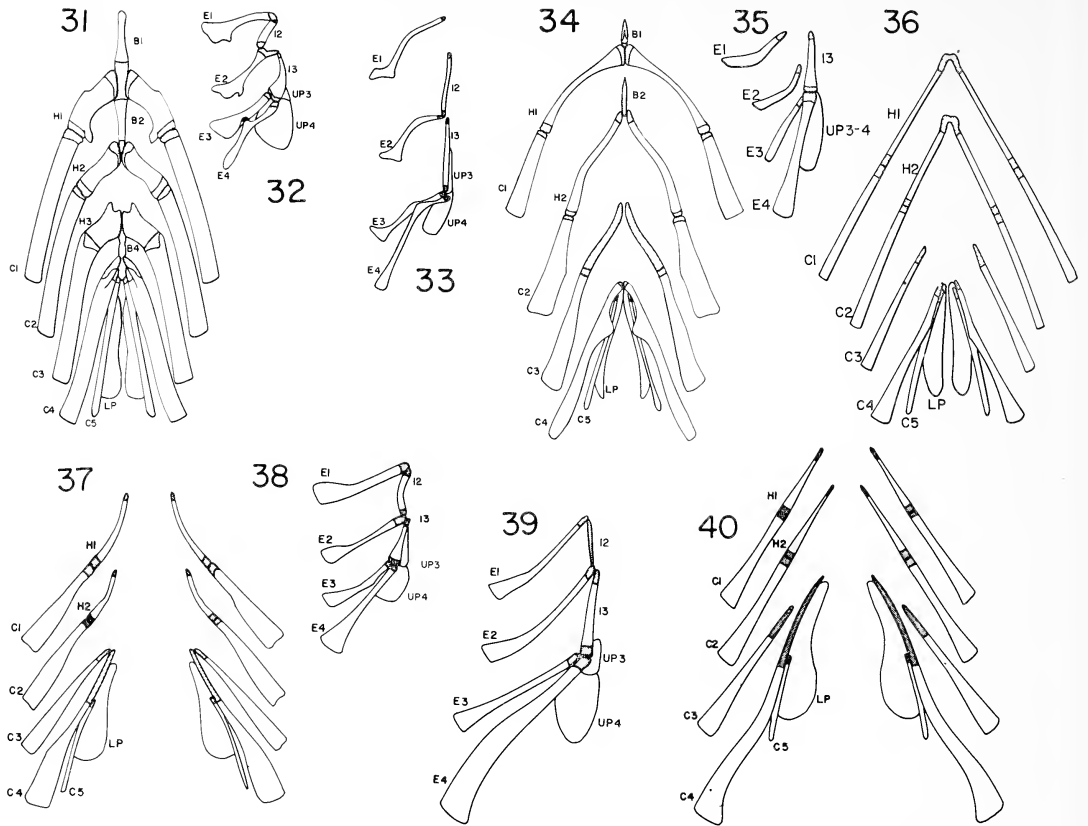
Specimens of *Ilyophis* have not been available for study. The genus is included in this lineage primarily on the evidence of Castle (1964), who included *Ilyophis* in the family Synphobranchidae.

Anguilloid Lineage

The arches of *Heterenchelys* and *Anguilla* (Figs. 31, 32) are quite similar and are the most generalized. All of the skeletal elements found in eels are present in *Heterenchelys*, while *Anguilla* lacks only B3 (Table 1). According to Norman (1926) even this element occurs in cartilaginous form in the embryo.

The arches of *Heterenchelys* are much nearer those of *Anguilla* than those of *Moringua* (Figs. 33, 34), which has them noticeably reduced, basibranchials being either rudimentary or absent. Dorsally, I2 has lost its usual connection with the proximal end of E1. Gill arch characters, therefore, suggest that *Heterenchelys* is more closely related to *Anguilla* than to *Moringua* (cf. Regan, 1912a:32).

The xenocongrids, *Dysommia*, and the muraenids are alike in having lost the entire basibranchial series. While the hypobranchials of either side retain midventral connections in *Dysommia* (Fig. 36), they are without such connections in the xenocongrids (Figs. 37–40) and muraenids (Figs. 41, 42). Among xenocongrids and *Dysommia*, C5 is present and ossi-



FIGS. 31–40. 31 and 32, *Anguilla rostrata*. 33 and 34, *Moringua javanica*. 35 and 36, *Dysommima rugosa*. 37 and 38, *Chilorhinus platyrhynchus*. 39 and 40, *Kaupichthys diodontus*.

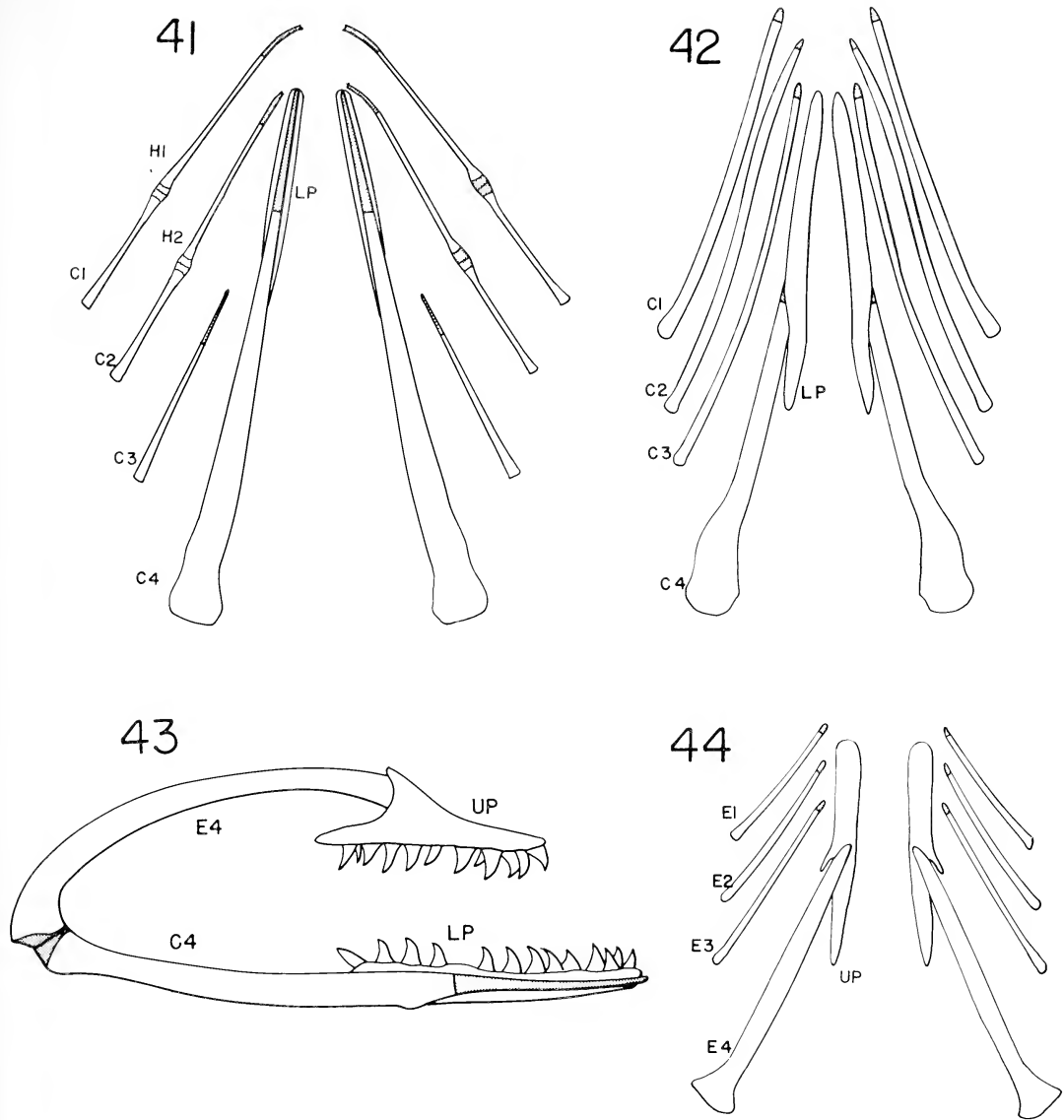
fied, although reduced in *Kaupichthys*. Among muraenids it is lost as an independent element.

Dorsally, the skeleton is complete in terms of number of elements in *Heterenchelys*, *Anguilla*, *Moringua*, *Chilorhinus*, *Chlopsis*, and *Kaupichthys brachychirus*. I2 is rudimentary in *K. diodontus* (Fig. 39) and absent altogether in *Dysommima* (Fig. 35) and the muraenids (Fig. 44). In *Dysommima* there is but a single upper tooth plate, probably representing a fusion of the two present in more generalized forms. In the muraenids the tooth plate is likewise single and apparently has fused with I3.

On the basis of gill arch characters, the xenocongrids, *Dysommima*, and the muraenids resemble one another more than they do other members of the lineage to which they presumably belong. *Dysommima* in this regard resembles the xenocongrids in having C5 well

developed and the lower pharyngeal tooth plates rather small and posterior in position, with small conical teeth in numerous rows. It is more generalized in having the hypobranchials interconnected, but more specialized in having lost I2 altogether and having the upper pharyngeal tooth plates in a single pair, as in the muraenids. For these reasons the arches of *Dysommima* seem intermediate in structure between those of the xenocongrids and muraenids (cf. Ginsburg, 1951; Böhlke and Hubbs, 1951).

Within the Muraenidae two structural types are apparent: one (Fig. 41), including only *Uropterygius*, *Anarchias*, and *Channomuraena*, has independent hypobranchials in the first and second arches. The lower pharyngeal tooth plates lie generally on the dorsal surface of the proximal end of C4. The other type (Fig. 42),



FIGS. 41–44. 41, *Uropterygius knighti*. 42, *Gymnothorax petelli*. 43, *G. petelli*, pharyngeal jaws of right side, lateral view. 44, *G. petelli*, dorsal view.

including *Muraena*, *Echidna*, *Gymnothorax*, and the remaining genera examined, are somewhat more specialized in gill arch structure, having lost all hypobranchials. The lower tooth plates tend to lie on the medial surface of the proximal end of C4, which fits into a prominent groove in the plate. These two groups may be considered as distinct subfamilies within the family Muraenidae.

UROPTERYGIINAE new subfamily

Ossified hypobranchials in first and second arches; lower pharyngeal tooth plates without a lateral groove; retractor ossium pharyngealium muscles without an attachment to the vertebral column; anterior portion of dorsal aorta usually enclosed in a canal formed by vertebral processes; vertical fins reduced, with rays confined to the posterior part of the tail.

Genera examined: *Uropterygius*, *Anarchias*, *Channomuraena*.

Subfamily MURAENINAE

No ossified hypobranchials in branchial skeleton; lower pharyngeal tooth plates with a prominent lateral groove; retractor ossium pharyngealium muscles with an attachment to the vertebral column; anterior portion of dorsal aorta not enclosed in a canal formed by vertebral processes; vertical fins not reduced, with rays confined to the posterior part of the tail.

Genera examined: *Echidna*, *Enchelycore*, *Enchelynassa*, *Evenchelys*, *Gymnomuraena*, *Gymnothorax*, *Muraena*, *Rabula*, *Strophidon*.

The outstanding feature of the gill arch skeleton of the muraenids is the enlargement of the fourth arch and with the loss of C5 the tooth-bearing bones it comes to support. Teeth on these bones are enlarged, recurved, and generally in two rows (Popta, 1904). These elements form the so-called pharyngeal jaws (Fig. 43).

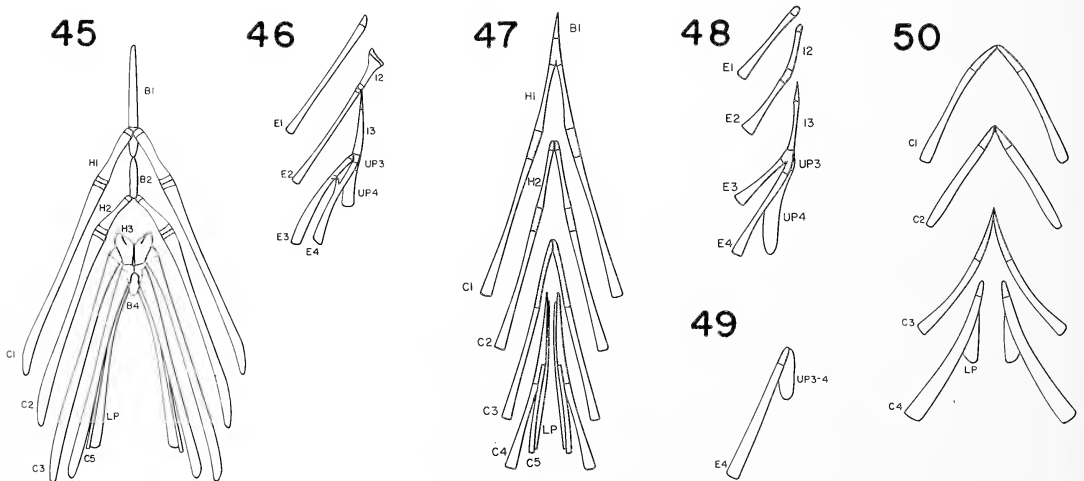
In view of the above, the structure of the gill arch skeleton of the muraenids, although specialized, is not sufficient to warrant the separation of this group at the ordinal or even sub-ordinal level from the other eels. Rather, stages in the derivation of the gill arches of the muraenids are suggested in the more generalized eels

of the same lineage. These exhibit the progressive loss of some bones, the fusion of others, the gradual enlargement of the fourth arch and the dermal tooth-bearing bones it comes to support.

Serrivomeridae and Nemichthyidae

The arches of *Serrivomer* (Figs. 45, 46), although somewhat specialized, are rather like those of *Anguilla*, especially as regards the loss of B3, and the form of H3. They are rather complete in terms of the number of elements, and generalized in retaining the double articulation of C4 with B4. The arches of *Avocettina* and *Nemichthys* (Figs. 47, 48) are somewhat more reduced but still relatively complete. They differ markedly from those of *Cyema* (Figs. 49, 50), which has the branchial skeleton severely reduced, more so than that of any other eel examined.

The systematic position of the eels of the families *Serrivomeridae* and *Nemichthyidae* (as interpreted by Böhlke and Cliff, 1956) has not yet been satisfactorily determined. Whether they are closely related families is open to some doubt (Trewavas, 1932:652; Berlin, 1942:108). The separate frontals and generalized gill arch characters of *Serrivomer*, however, suggest that this form may represent an early offshoot from the anguilloid lineage. The condition of the frontals in the *Nemichthyidae* is variable, some members having them fused,



FIGS. 45-50. 45 and 46, *Serrivomer sector*. 47 and 48, *Nemichthys scolopaceus*. 49 and 50, *Cyema atrum*.

others separate. The consensus seems to favor the view that the group is a natural one. The dorsal parts of the gill arches in *Nemichthys* bear some resemblance to those of *Serrivomer*, whereas the ventral parts in *Nemichthys* are somewhat more reduced, paralleling perhaps the trend toward reduction in other eel groups. Thus, gill arch structure may be consistent with the opinion that these two families are closely related, but can neither confirm nor refute this opinion. In any event, the Nemichthyidae is here included in the anguilloid lineage for want of clear evidence to the contrary.

Functional Significance of Gill Arch Modifications in Eels

Much could be said concerning the functional significance of the various types of gill apparatus found among the eels. The following remarks concern one possible interpretation of some of those of the anguilloid lineage.

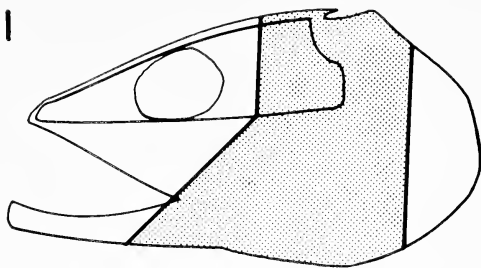
In generalized teleosts, the cranium, jaws, and gill arches form closely integrated parts of a mechanical system functioning to seize prey organisms. The functional roles of the parts of this system have been analyzed by several authors (Höller, 1935; Hofer, 1945; Tchernavin, 1947, 1953; Kirchhoff, 1958; Kampf, 1961; and others). The functional interdependence of these parts is dependent on their near relative positions. In such generalized teleosts as *Elops* and *Epinephelus*, the gill arches are located close behind the jaws, more or less beneath the posterior part of the cranium (Figs. 51, 52).

In the eels, however, the arches are posteriorly displaced from a position beneath the cranium to a position behind it. This displacement is slight in *Conger*, moderate in *Anguilla* and *Chilorhinus*, and extreme in *Gymnothorax* and *Moringua* (Figs. 53–57).

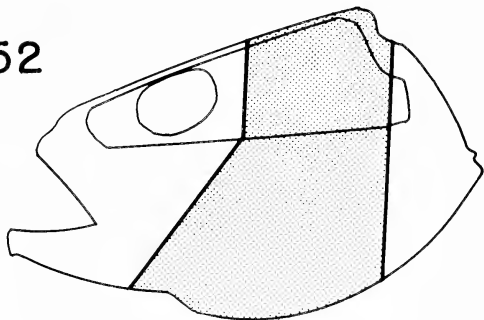
Probably as a result of this displacement, both the pectoral girdle and the gill arches lost the attachments to the cranium characteristically present in other teleosts. In the case of the gill arches, this attachment occurs through the first pharyngobranchial. In the case of the pectoral girdle, it is through the posttemporal. Both of these bones are absent without known exceptions among the eels.

It seems likely that the position of the gills

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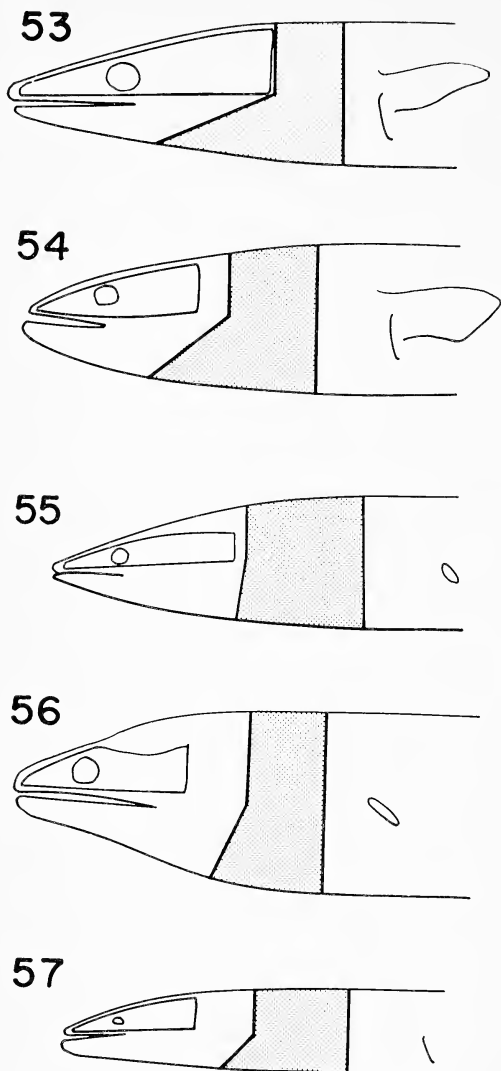
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FIGS. 51 and 52. 51, Position of branchial region in relation to cranium and jaws of *Elops hawaiiensis*. "Branchial region" denotes that space bounded anteriorly by the dorsal and ventral proximal ends of the first arch, posteriorly by the rear border of the dermal tooth plates. 52, *Epinephelus fuscoguttatus*.

is not without some functional significance. The habits of eels, of wedging themselves through crevices or burrowing in the sand, seemingly require an eel-like body, long and narrow, especially in front. Reduction in head diameter seems to have been achieved in part by the movement posteriorly of the gill arches from a position beneath the cranium to one behind it. In this connection, the degree of elongation—the relation between body length and diameter—seems to be correlated with the posterior displacement of the gill region (Fig. 58).

With the arches posteriorly displaced, they tend to lose their role in seizing prey, which then is left to the jaws and cranium alone. This loss in function perhaps may account for the obvious trend toward the loss of certain gill arch elements among eels. This entails the loss of firm interconnections between the gill skeleton and the cranium, between successive arches of the gill skeleton, and between the paired elements of either side. Each of these losses tends



FIGS. 53-57. 53, *Conger marginatus*. 54, *Anguilla rostrata*. 55, *Chilorhinus platyrhynchus*. 56, *Gymnothorax eurostus*. 57, *Moringua javanica*.

to augment the expansibility of the pharynx, which is of obvious significance to an eel-like fish. Interestingly, many of these same modifications have occurred independently among syngnathiform fishes (Jungerson, 1910; Rauther, 1925) and symbranchiiform fishes (personal observation), possibly also as a result of spatial separation of jaws and gill arches.

The functional significance of the so-called pharyngeal jaws of the morays and other forms remains to be commented on. On the basis of the nature of the teeth and the branchial

musculature, which is to be discussed elsewhere (Nelson, MS), these prominent tooth-bearing bones apparently function in moving food from the jaws into the esophagus. They have developed, it seems, in relation to mechanical problems involved in moving relatively large food organisms through a secondarily elongate pharynx.

Remarks on Eel Origins

For several reasons, eels are customarily regarded as isospondylous derivatives, and, because of larval features, as being particularly close to the elopoids. Some gill arch characters of eels also suggest an isospondylous origin: (1) pharyngeal tooth plates are generally not fused with underlying endochondral bones, (2) the lower pharyngeal tooth plates are sometimes multiple, (3) retractor ossium pharyngealium muscles are without an attachment to the vertebral column except among some muraenids (Nelson, MS).

Among teleosts above the isospondylous level, pharyngeal tooth plates are generally fused with their endoskeletal supports, and the lower ones are in a single pair (Nelson, MS). Retractor muscles with an attachment to the vertebral column probably are present in all forms above the isospondylous level (Dietz, 1912, 1914, 1921; Holstvoogd, 1960, 1965).

One striking difference between the arches of isospondylous fishes and eels is that in most of the former prominent tooth plates overlie the basibranchials, while no such plates are present in any of the eels examined. These, however, may be presumed to have been lost in relation to the posterior displacement of the arches.

In view of this peculiarity of the gill arch skeleton in eels, no striking resemblance between it and that of any of the major groups of isospondylous fishes can be demonstrated. One feature, however, may deserve mention. This concerns the loss of medial processes on the pharyngobranchials of eels. These processes are important supports for the upper pharyngeal bones in most teleosts (Nelson, MS). They are absent, however, on the third pharyngobranchial of *Albula* among elopoids (but not of *Megalops*, *Elops*, or *Pterothrissus*), and in at least *Aldrovandia* among halosaurids (per-

sonal observations). Perhaps the tendency toward the reduction of these processes may be evidence of genetic relationship.

SUMMARY

1. On the basis of gill arch and other characters the eels may be divided into at least three evolutionary lineages: anguilloid (Anguillidae, Heterenchelidae, Serrivomeridae, Nemichthyidae(?), Moringuidae, Xenocongridae, Dysommidae, Muraenidae), synphobranchoid (Synphobranchidae, Ilyophidae, Simenchelidae, Dysommidae), and congroid (Congridae, Heterocongridae, Nessorhamphidae, Nettastomidae, Derichthyidae, Ophichthidae, Muraenesocidae).

2. In each of these lineages the gill arches seem to have been similarly modified through (a) the progressive enlargement, or reduction with eventual loss, of skeletal parts, (b) simplification in form of the skeletal parts (loss of grooves and processes), (c) an anterior shift in position of the lower pharyngeal tooth plates, which gradually become supported by the fourth rather than fifth ceratobranchials.

3. Within the anguilloid lineage the Heterenchelidae and Anguillidae are the most generalized in gill arch structure. *Moringua* is somewhat more specialized. The Xenocongridae, *Dysommia*, and Muraenidae resemble one another more than they do other members of this lineage. The Muraenidae have the gill arches most highly specialized, and on the basis

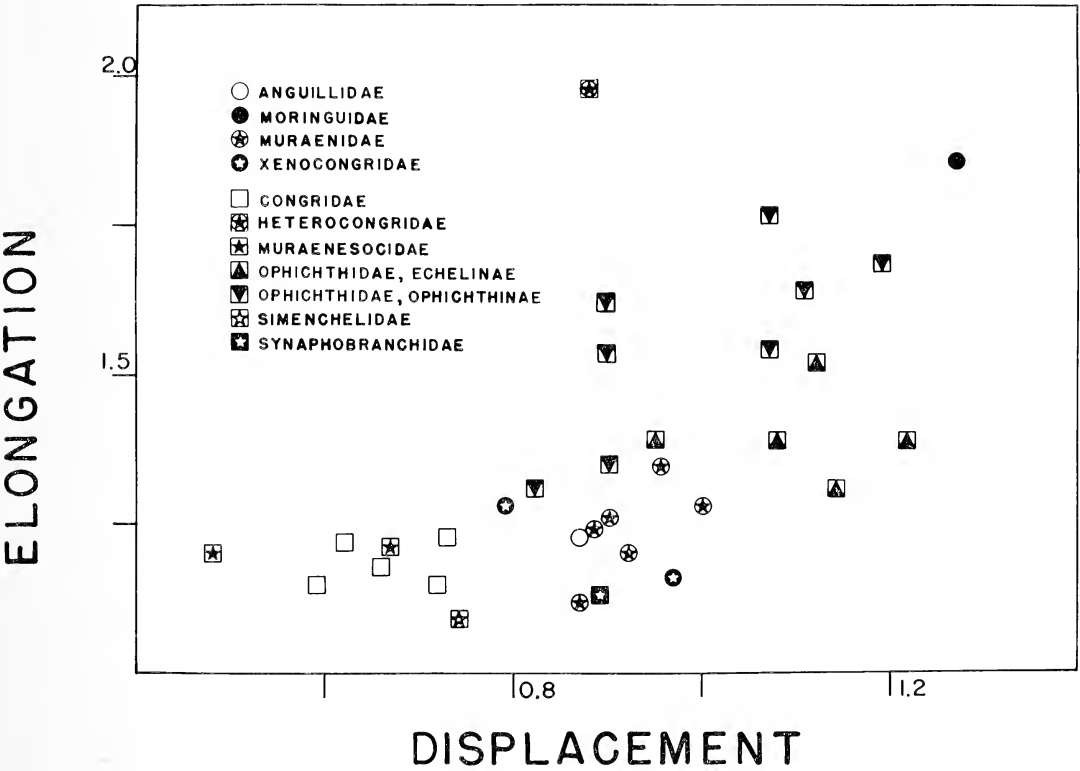


FIG. 58. Scatter diagram showing correlation between body elongation and posterior displacement of the branchial region in selected representatives of some eel families. Elongation = log body length/maximum body diameter. Displacement = log 10 x postcranial head length/cranial length. Example: for *Moringua javanica* the following measurements were taken: total length 805 mm, maximum body diameter 11 mm, head 49 mm, cranium (snout tip to posterior limit of cranium) 17 mm.
Elongation = log 805/11 = 1.86
Displacement = log 320/17 = 1.27
Measurement data on other species will be furnished by the author on request.

of gill arch and other structures may be divided into two subfamilies, one of which is proposed as new, Uropterygiinae and Muraeninae. The arches of *Serrivomer* are sufficiently similar to those of *Anguilla* to suggest a relationship between these forms. Those of nemichthyids are somewhat reduced (*Nemichthys*, *Avocettina*) or severely reduced (*Cyema*).

4. The members of the synphobranchoid lineage are alike in having the third hypobranchials posteriorly directed.

5. Within the congrid lineage most of the members have a well ossified and complete gill arch skeleton. The only major exceptions are found among the Ophichthidae, whose members show great variability in gill arch structure.

6. Gill arch modifications seem related to body form and habits of eels. The gills are posteriorly displaced in the more elongate forms. Loss of skeletal elements has resulted in many eels in a highly expandible pharynx, seemingly an adaptation for swallowing large prey. The development of "pharyngeal jaws" in the more highly specialized eels seems related to mechanical problems of moving relatively large prey through a secondarily elongate pharynx.

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Comments on the Classification of the Percoid Fishes¹

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IN TERMS OF DIVERSIFICATION, the Perciformes is by far the most successful of fish orders, maximally represented in the inshore waters of tropical seas. Thus, of the 130 families of native Hawaiian fishes, some 41 belong to the Perciformes, and 18 belong to the single superfamily Percoidae, which forms the subject of the present paper.

From the point of view of classification, the order Perciformes suffers from an overabundance of representation. In fish groups that have undergone extensive extinction the modern members may be unrepresentative, but at least the gaps between them are usually spacious, providing abundant material for the construction of discrete taxonomic pigeonholes. In the Perciformes, however, the results of repeated adaptive radiations seem to be living today. Some of these have led to a relatively high and complex structural reorganization (the "mesoevolution" of Dobzhansky, 1954). Where this has happened, it is comparatively easy to sort lineages. But after the major lines of evolution have been extracted (as separate orders, suborders, or superfamilies), the remaining basal percoids seem to represent a central theme with numerous variations.

Contributions toward our present knowledge of the percoid fishes have been made from a number of viewpoints, all of value. Jordan's classification (1923) is based primarily on external characters, whereas that of Regan (1913) relies heavily on the superb series of skeletons in the British Museum. In recent years more intensive investigations have been undertaken from two viewpoints. One is to trace a particular structure or structural complex through a broad sampling of percoid fishes. This has been done for otoliths by Frost (1927, 1928), for the predorsal bones and subocular shelf by Smith and Bailey (1961 and 1962, respec-

tively), for the caudal skeleton by Gosline (1961), and for the recurrent facial nerve by Freihofer (1963). The other approach is to study as many characters as possible in a particular percoid group, e. g., the Japanese seranids (Katayama, 1959) and carangids (Suzuki, 1962).

The present investigation began as an effort to ascertain the systematic position and relationships of a few percoid genera. It soon became apparent that, except within the narrowest limits, this was impossible without some overview of percoid classification as a whole. This paper is an effort to bring data on the supra-occipital crest and the jaw mechanism to bear on a general percoid classification and to rescue some main outlines of such a classification from the amorphous condition into which they have deteriorated as a result of the widely varied opinions recently expressed on the subject.

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PERCIFORM ORIGINS

The perciform fishes are generally believed to have arisen among the Beryciformes. Their success, as compared to that of the Beryciformes or indeed of any other order, cannot be attributed to any one major advance, but seems to be the result of an assimilation and integration of a number of minor improvements over beryciform features. Among the characters separating the Perciformes from the Beryciformes, some of the better documented are:

(1) Pelvic fins with no more than 5 soft rays. However, *Channa* (*Ophiocephalus*) has 6 segmented rays, and the flatfishes, presumably derived from the Perciformes, have up to 13 (Norman, 1934).

(2) Pelvic bones extending between and directly attached to the cleithra. The several exceptions to this seem to fall into two categories (Regan, 1909): those groups some or all of which seem never to have attained such an attachment—the Mugiliformes, Anabantidae, Channidae, and *Nannatherina* (Regan, 1940); and those groups in which some or all of the species seem to have secondarily lost such an attachment—Stromateidae, Tetragonuridae, Gempylidae, and Trichiuridae.

(3) Orbitosphenoid, antorbital, and nodules between the pelvic fin rays and the pelvic girdle absent as separate entities. There is no known percoid that retains any of these bones in the adult. Such bones, all present in the beryciform family Holocentridae, have been lost, however, in numerous fishes besides the Perciformes.

(4) Branched caudal rays 15 or fewer. Reduction in the number of branched caudal rays in the percoids is rather commonplace. A few round-tailed forms are known to have more than 15 (Gosline, 1960).

(5) In the percoids, as contrasted with most beryciform fishes, there are basically five circumorbital bones behind the lacrimal, and a subocular shelf, if present, tends to be restricted to the second (but see Katayama, 1959: Figs. 3–5). In the Beryciformes, except Holocentridae, there appear to be only four circumorbitals (Patterson, 1964), and the subocular shelf tends to spread over more than one of them. In this character, as in the generally high degree of ossification, it is the berycoids that seem to be

unusual as compared with other acanthopteran fishes (see below).

That an integration of the above characters did not occur all at once is shown by the groups of modern fishes which seem to have stopped short part way along the path of beryciform-perciform evolution: e. g., the Mugiliformes, anabantoid-channoid group, and apparently *Nannatherina* (see above paragraphs).

It has generally been postulated, implicitly or expressly, that the Perciformes has had a single origin among the Beryciformes. In 1964, however, Patterson suggested four separate origins for perciform families among the Beryciformes. Specifically these are:

BERYCIFORM ANCESTORS	PERCIFORM DERIVATIVES
Polymixiidae —————→	Scorpidae, Monodactylidae, and Kyphosidae
Sphenocephalidae —————→	Serranidae
Aipichthyidae —————→	Menidae and Carangidae
Pharmacichthyidae —————→	Acanthuroidei
Pycnosteroideidae — ? →	Chaetodontidae
Dinopterygidae — ?? →	Centrarchidae

Thus, according to Patterson's view the basal percoid families would have at least three and possibly five independent derivations from the Beryciformes, and the Acanthuroidei would have evolved from a sixth. Such a viewpoint deserves discussion in considerable detail.

Thanks to Patterson's (1964) excellent re-descriptions and figures of the Cretaceous berycoids *Berycopsis*, *Homonotichthys*, *Hoplopteryx*, and *Caproberyx*, it is possible to make a detailed comparison between these forms and the better known of modern berycoids (Starks, 1904). They fit together nicely. Thus *Berycopsis* and *Homonotichthys* belong in the same family with the modern *Polymixia* (Starks, 1904); *Hoplopteryx* with the modern *Trachichthys*; and *Caproberyx* with the modern holocentrids. These Cretaceous and modern forms together make up a sort of central core of the known Beryciformes, forming a congruent, easily recognizable, and clearly definable group of fishes. Thus, when Patterson suggests *Berycopsis*, a Cretaceous polymixiid that he has described in detail, as an ancestral type for the percoid families Scorpidae, Monodactylidae, and Kyphosidae, what he is saying is clear. Unfortunately,

both today and in the fossil record, little-known beryciform-like fishes lead out in all morphological directions from the central berycoid core. Patterson's other suggested points of origin for percoids are not core berycoids, but rather are peripheral forms for which little knowledge is available: *Sphenocephalus*, *Aipichthys*, the Pycnosteroididae, and the Dinopterygidae. What is known about these four groups gives me, at least, no feeling of assurance about even their beryciform affinities. Indeed, the various percoids Patterson suggests as separate derivatives from them (Serranidae, Menidae and Carangidae, Chaetodontidae, Centrarchidae) would seem to me to be a far more close-knit group than the various forms from which they were supposedly derived.

That some of the lesser known, "peripheral" fossil berycoids like *Aipichthys*, *Sphenocephalus*, *Dinopteryx*, and *Pycnosteroides* may prove to be nearer the ancestral percoid type than the "core" berycoids seems quite probable, if only because the reduction in ossification which may well have led to the lack of knowledge of the "peripheral" berycoids is also a step in the direction of the percoids. Stated conversely, the "core" berycoids, except possibly the Polymixiidae, seem to be too completely ossified to have been percoid ancestors.

So far the objections to deriving different basal percoids from separate berycoid stocks have been of a general nature. Some discussion of the supraoccipital crest will, I think, provide evidence against certain of the specific derivations postulated by Patterson.

The supraoccipital crest attains extensive development only in the teleosts. Among lower teleosts the supraoccipital tends to be a small bone at the rear of the skull that does not extend forward between the parietals. In general, the size of the supraoccipital bone is quite closely associated with the size of its crest: where the crest is large the supraoccipital is large, and in groups where the crest is low or lacking the supraoccipital may disappear, as in some congrid eels. In the acanthopteran fishes the supraoccipital crest may become very large; here the deeper-bodied fishes tend to have larger crests.

Among deep-bodied fishes, however, there are two quite different types of crest and,

though each has doubtless arisen many times, it seems improbable that one would give rise to the other. In strongly swimming, compressed fishes the body musculature tends to extend far forward over the head. This musculature has its attachment in large part to the supraoccipital crest which extends forward within it. In the berycoid *Homonotichthys* (Patterson, 1964:284, fig. 35) and in numerous percoids the supraoccipital comes forward between the frontals or its crest extends forward over the frontals. In a whole series of percoid families, including the Carangidae, Coryphaenidae, and Priacanthidae, an even greater anterior extension of the supraoccipital crest is brought about by the development of a median ridge on the paired frontals. In all these fishes the crest is buried in musculature and is not broadly exposed on the surface, its upper rim being more or less knife-edged. Finally, the cranial roof below the crest is not especially vaulted or otherwise distended.

A quite different type of supraoccipital crest, constructed in another way and serving another principal function, is that of the acanthuroids, chaetodontids, *Antigonia*, etc. Here, in essentially slow-moving, spinous fishes, the supraoccipital extends up and back over the nape as a sort of protective shell. (This same type of development is found in some of the lower teleosts, e.g., catfishes.) One can envision this construction as arising from the condition in fishes like the modern berycoids *Holocentrus* or *Myripristis*. In these the supraoccipital crest is small and extends directly back from the upper surface of the skull; its upper border has flattened out somewhat. If, in deeper-bodied forms such as the extinct holocentrid *Caproberyx*, this type of supraoccipital crest, along with the whole posterior portion of the cranium, were to be raised up and expanded over the nape, then the development of a posteriorly vaulted skull continued up and back as a rooflike supraoccipital crest would occur. In such a fish as *Chaetodon*, which has this type of construction, there is very little muscle attachment to the high, broad, and strong supraoccipital crest. The vaulting at the rear of its cranium adds structural strength to the crest base (and also has the curious result of leaving the brain resting in the bottom of a high, empty vault).

Thus *Chaetodon* and *Caranx*, representing the two extreme types of supraoccipital just described, both have high crests, but structurally and functionally they are far apart. Furthermore, the two extremes represent quite different modes of life in the fishes that bear them. Any combination of them seems unlikely. Nor does it appear that one could be developed from the other except by going all the way back through some intermediate form with a relatively small, unspecialized occipital crest. Yet among Patterson's derivations, he has the sharp-crested carangids and menids arising from *Aipichthys*, which according to his illustration (1964: Fig. 83) seems to have a chaetodontid-type (roofed) occipital process. Similarly, *Sphenocephalus*, which Patterson has as a progenitor of the Serranidae, appears (Patterson's Fig. 78) to have the broad-roofed crest of *Chaetodon*, not the cutting edge found in the serranids (Katayama, 1959). If the preceding analysis of supraoccipital crest development is sound, both of these derivations of Patterson's would seem most improbable.

But to belabor Patterson's individual derivations is probably overshooting the mark, for at the present time I see no reason to look nearly as far back as the berycoids for a percoid progenitor. It seems to me, rather, that some one berycoid lineage could have evolved a fairly long way, i.e., could have developed most of the characters listed previously, before branching into the various percoid lineages, or even before giving off such subpercoid groups as the Mugiliformes. In short, I am far more impressed by the differences between the berycoids and the percoids, or among the berycoids themselves, than by those between the various percoids.

THE ARRANGEMENT OF PERCOID FAMILIES

The 50 or so families of fishes included in the superfamily Percoidae have been grouped in various ways. Data on feeding and on jaw structure to be presented below support an arrangement proposed by Regan in 1913. In that paper Regan merely took up the families in serial order. However, in his introductory statement (1913:113) he said: "In the following arrangement a few of the more aberrant fami-

lies are placed last, and the remainder are grouped into those without (Serranidae to Coryphaenidae) and those with a scaly process in the axil of the pelvic fins." The process in question is made up of one to several modified scales that form a pointed projection extending back between the lateral border of the pelvic spine and the body. Among acanthopteran fishes the process occurs in some but not all members of the Beryciformes and Mugiliformes, and in the Perciformes it occurs among the Percoidae, Pomacentroidae, and Labroidae (Table 1). In the Percoidae the axillary process can be postulated as being an independently developed or as an inherited character. Since there is no indication that the axillary processes of the Beryciformes, Mugiliformes, and Perciformes are not homologous, it seems more satisfactory to postulate that the percoid process has been lost one to many times in the families in which it is lacking (Table 1), rather than that a structure found in the Beryciformes and Mugiliformes has been lost and then redeveloped in certain members of the Percoidae. Within percoid families the axillary process, when present, is fairly constant; exceptions are the Centropomidae (Weber and deBeaufort, 1929:393), Sciaenidae (Norman, 1957:219), and Chaetodontidae (Fraser-Brunner 1946:466). Percoid families with and those without axillary scales are listed in Table 1. "Above" the Percoidae axillary processes are found, to the author's knowledge, only among the perciform superfamilies Pomacentroidae and Labroidae.

It would seem that those families without and those with an axillary process are characterized by two rather different modes of feeding. Percoid families without an axillary scaly process generally engulf their food, so to speak. Either the fish simply runs down its prey, merely opening its mouth at the appropriate moment, or food organisms in close enough proximity are sucked into the mouth by sudden expansion of the oral and branchial cavities. In either event the main problem is to get the jaws *open* at the right time, and the chief function of the unspecialized teeth is merely to grasp the prey. By contrast, the perciform families with an axillary process tend to specialize in the direction of selecting their food items with their front teeth. They may pluck it out from its

surroundings, as the chaetodontids and labrids do, or nip it off, as the scarids do. Their main problem is to get the mouth effectively *shut* over the selected item, and their front teeth are often specialized in various ways.

In the above analysis two quite different methods of feeding have been contrasted. However, among the less specialized percoids a fish that habitually feeds in one of these two ways may shift more or less easily to the other, and many percoids are opportunists, eating what they can find in whatever manner they can get it.

The jaw mechanisms in the two groups just differentiated reflect their main feeding habits (or vice versa). Certain general attributes of jaw structure are held in common by all percoid fishes. Among these are the (usual) abilities (1) to bring the maxillary down across the corner of the mouth when the lower jaw is swung open, (2) to protrude the premaxillaries, and (3) to expand the oral cavity laterally as well as vertically.

Although the more generalized percoids are quite similar to one another in jaw structure, rather different trends of development from this basal pattern are discernible in those fishes with, and in those without, an axillary process. In the "engulfing" forms (without an axillary process) the teeth do not become specialized and the jaw structure develops in one of two directions. In such fishes as the carangid *Scomberoides* (or *Chorinemus*), which simply runs down its prey, premaxillary protrusion has been lost and the maxillary has become a simple strut above the premaxillary (Suzuki, 1962: Fig. 15F). In contrast, the serranid fishes of the genus *Epinephelus* perhaps represent the epitome of a trend toward a cavernous mouth opening.

A comparison between *Epinephelus spilotoceps* (without an axillary process) and *Lutjanus vaigiensis* (with an axillary process) may serve to exemplify the differences between the two groups. In specimens of both species 140–155 mm in standard length the width of the gape is about the same when the mouth is closed (14–15 mm), yet when the mouth is opened wide the gape expands laterally only to 18 mm in *Lutjanus* but becomes a yawning chasm 30 mm across in *Epinephelus*. One factor that makes possible the relatively wide gape opening is the

TABLE 1

FAMILIES WITH A SCALY PROCESS IN THE AXIL OF THE PELVIC FIN	FAMILIES WITHOUT A SCALY PROCESS IN THE AXIL OF THE PELVIC FIN
Beryciformes	Beryciformes
Polymixiidae	Trachichthyidae
Holocentridae	
Mugiliformes	Mugiliformes
Mugilidae	Sphyraenidae
Atherinidae	
Polynemidae	
	Zeiformes
	Antigoniidae
Perciformes	Perciformes
Percoidei	Percoidei
Percoidae	Percoidae
Centropomidae	Percichthyidae
Bramidae	Serranidae
Pempheridae	Plesiopidae
Arripididae	Acanthoclinidae
Lutjanidae	Kuhliidae
Scorpididae	Centrarchidae
Nemipteridae	Priacanthidae
Pomadasyidae	Cepolidae
Toxotidae	Rainfordiidae
Monodactylidae	Apogonidae
Lobotidae	Percidae
Lethrinidae	Lactariidae
Kyphosidae	Labracoglossidae
Dichistiidae	Bathyclupeidae
Girellidae	Pomatomidae
Sparidae	Rachycentridae
Centracanthidae	Carangidae
Emmelichthyidae	Menidae
Leiognathidae	Coryphaenidae
Sciaenidae	Nandidae
Mullidae	Cichlidae
Chaetodipteridae	Sillaginidae
Drepanidae	Branchiostegidae
Scatophagidae	Cirrhitidae
Chaetodontidae	Cirrhitidae
Enoplosidae	Cheilodactylidae
Histiopteridae	Trachinoidae
Oplegnathidae	Parapercidae
Pristolepidae	Embiotocidae
Pomacentroidae	Embiotocidae
Pomacentridae	Notothenioidae
Labroidae	Nototheniidae
Labridae	Acanthuroidei
Scaridae	Acanthuridae
	Zanclidae
	Siganoidae
	Siganidae
	Scombroidei
	Scombridae
	Stromateoidei
	Nomeidae
	Anabantoidei
	Anabantidae

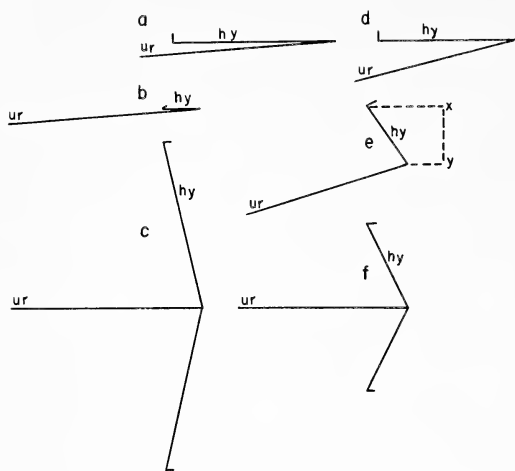


FIG. 1. Movement of the hyoid apparatus in *Epinephelus spilotoceps* (a-c) and *Lutjanus vaigiensis* (d-f). Diagrammatic side view with the mouth shut (a, d) and the mouth open (b, e), and top (or bottom) view with the mouth open (c, f). Head of fish to the right. *hy*, Hyoid bar; and *ur*, urohyal. The distance *xy* indicates the amount of potential lateral expansion lost in *Lutjanus* by the downward pull of the urohyal.

much longer jaws. In *E. spilotoceps* 140–150 mm long the length of the upper jaw to the end of the maxillary is 32 mm and that of the lower jaw is 40 mm; these same dimensions for *L. vaigiensis* are only 21 and 23 mm. If the longer jaws of *Epinephelus* create the possibility of greater gape expansion they do not ensure it per se. (Fishes with the longest jaws quite frequently have a rather narrow gape, e.g., *Lepisosteus*, *Belone*.) In *Epinephelus* there are three ways in which gape expansion is actually accomplished. First, the lower rims of the suspensoria may be swung out from the cranium by contraction of the levator hyomandibularis et arcus palatini (van Dobben, 1935:7, 8). Second, contraction of the sternohyoideus pulls the urohyal backward (Fig. 1) and in so doing forces the posterior portions of the epihyals out laterally (van Dobben, 1935:8). Finally, a twisting of the maxillary shaft rolls its lower border, and with it the lateral end of the premaxillary, somewhat outward away from the head in *Epinephelus*, as in *Perca* (van Dobben, 1935:11).

Epinephelus and *Lutjanus* show differences in all three of these processes. That having to

do with the spreading of the suspensoria by way of contraction of the levator hyomandibularis et arcus palatini is merely one of degree: in *Epinephelus* this muscle appears to be much broader and more powerful than in *Lutjanus*. (The dilatator operculi, which is instrumental in expanding the gill cavity, is also much larger in *Epinephelus* than in *Lutjanus*.)

So far as the hyoid bar method of gape expansion is concerned, there are differences both in degree and in the direction of the forces. In the first place, *Lutjanus* has hyoid bars that are only two-thirds as long as those of *Epinephelus*, so that the potentiality for lateral expansion is only two-thirds as great. But even allowing for this difference, the hyoid bars are not forced out to their maximum lateral expansion in *Lutjanus* when the mouth is opened. In *Epinephelus* (Fig. 1a-c) contraction of the sternohyoideus pulls the urohyal (Fig. 1, *ur*) almost straight back, forcing the posterior ends of the hyoid bars directly outward. In *Lutjanus* (Fig. 1d-f), however, as in most deep-bodied fishes, contraction pulls the front of the hyoid bars backward and downward, and some of the potential lateral thrust is lost in the downward motion (the amount equal to *xy* in Fig. 1e).

Though the hyoid bar factors just mentioned would seem to play the greatest quantitative role in the difference in lateral gape expansion between *Epinephelus* and *Lutjanus*, the feature showing the largest qualitative difference is the twisting or nontwisting of the maxillary shaft when the mouth is opened. In both *Lutjanus* and *Epinephelus* a ligament from the adductor mandibulae and the lower jaw runs to an attachment on the outer surface of the maxillary shaft anteriorly (Fig. 2, *L*). In narrow-mouthed fishes, when the adductor contracts this ligament helps to pull the maxillary up and back to the closed-mouth position. In wide-mouthed fishes it has a different function when the gape is widely opened: as the posterior end of the maxillary swings laterally with gape expansion, the ligament comes to pull across it, causing the maxillary to rotate on its shaft (Fig. 2). This rotation at the anterior end of the maxillary causes protrusion of the premaxillaries; posteriorly it rolls the lower border of the maxillary outward, and with it to some extent the lateral ends of the premaxillary, thus

expanding the already broad gape even farther.

The tremendous expansion of the open gape of *Epinephelus* seems to be at the end of one trend of jaw development. However, almost the same jaw construction and capabilities occur in the Beryciformes (e.g., *Holotrachys*), Scorpaeniformes (e.g., *Scorpaenopsis*), etc. A fish with this type of jaw construction would seem well adapted to engulfing nearby objects of moderate to large size, especially those close to the bottom. There are, however, a number of things such a fish will not be able to do well. It has no method of selecting one particular food item from its immediate surroundings. Nor can it bite off a part of anything, e.g., a fisherman's bait. Finally, such a fish probably cannot bite down on anything with much force; the length of the jaws militates against this, especially since the partly rotated maxillaries do not form a very firm support for the

lateral ends of the premaxillaries when the mouth is open.

Among perciform fishes with an axillary scaly process there are some basal families, e.g., Centropomidae, Pempheridae, Bramidae, and perhaps Sciaenidae, in which no particular jaw specialization is apparent. But in the other families there is a notable trend toward a single row of specialized teeth. Sometimes, as in the chaetodonts, these teeth are hairlike and are used for such purposes as separating the eggs of other fishes from the rocks on which they have been laid. In other families the teeth may be incisiform (Kyphosidae, Pomacentridae), molariform (Sparidae), or fused into a beak (Oplegnathidae, Scaridae). Whatever the type of teeth, there are several features of head structure held in common by the more advanced perciform fishes with axillary scales. One is that the mouth is always relatively small, with comparatively little lateral expansion. The maxillary is more or less restricted to a single plane of movement, sliding up and down directly above the lateral ends of the premaxillary; it often forms a sort of cap fitting over the tip of the premaxillary, and in its most extreme development, i.e., in the Scaridae, the maxillary becomes rigidly united to the premaxillary. With the restriction of the lateral expansion of the gape, the lacrimal (preorbital) frequently extends down over the maxillary and premaxillary, completely covering them when the mouth is closed, e.g., as in *Lutjanus*. This lacrimal expansion helps restrict the maxillary below it to a single plane of movement and inhibits rotation of the maxillary; it also carries openings of the lateral line canal down to just alongside the mouth (along the lower border of the expanded lacrimal). Finally, as the fishes in this group become smaller-mouthed, the mouth tends to move downward and forward and the eye up and back on the head. Sometimes, as in the labrid *Gomphosus*, the mouth seems to operate somewhat on the principle of long-handled forceps, or again, as in the labrid *Epibulus*, on the principle of a bellows.

The jaw differences between the two main types of percoid fishes discussed in the preceding paragraphs are summarized in Table 2.

In this paper an association has been postulated between certain aspects of feeding and an

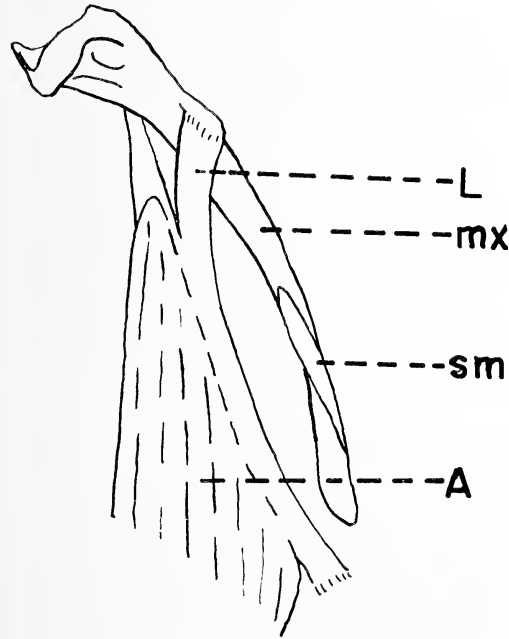


FIG. 2. Maxillary and associated features in *Epinephelus* with the mouth open, superior view. A, Adductor mandibulae muscle; L, ligamentum maxillo-mandibulare posterius of van Dobben (1935:Fig. 5): anteriorly it joins a ligament to the inner surface of the maxillary, above it is joined by a sheath to the adductor mandibulae, and posteriorly it is attached to the lower jaw (not shown); mx, maxillary; and sm, supramaxillary.

arrangement of families proposed by Regan ostensibly on the basis of the axillary scaly process. This postulate requires amplification and clarification in several respects.

In the first place, it has been hypothesized that the presence of an axillary process is an inherited character and that its loss in the percoids has been secondary. On the other hand, those fishes that have retained the process include the forms which have developed much the most specialized jaw structure. I can see no causal explanation for this divergence of evolutionary direction and must fall back on the fact that functionally independent and nonpleiotropically controlled characters evolve independently. It may be instructive, therefore, to discuss separately the assumed evolutionary sequence in axillary process loss and jaw structure specialization.

Axillary processes, if inherited in percoids as here believed, would seem to have been lost many times under varied circumstances. Among the Beryciformes a minute-scaled *Paratrachichthys* lacks axillary processes, as do all other groups known to me that have very small scales or none at all. Among the Mugiliformes *Sphyræna* lacks axillary processes; and, whether there is a causal relationship or not, all fast-swimming fishes except the Bramidae and Pempheridae lack processes, e.g., Carangidae, Coryphaenidae, Scombroidei. Again, all fishes that prop themselves off the bottom by the pelvic fins lack axillary scales, e.g., Blenniidae, Cirrhitidae as well as all fishes that have modified

or reduced pelvics, e.g., Gobioidae, Ophidioidae. Indeed, since apparently all families above the Percoidae except the Pomacentroidae and Labroidae lack axillary processes, the major problem is perhaps that of why so many percoid families have them. To this question there is, to my knowledge, no answer worth writing.

A related matter for which I know no solution is why Regan (1913) excluded "a few of the more aberrant families" from his division between those percoids with, and those without, an axillary process. The families so excluded are apparently the Cepolidae, Cichlidae, Oplegnathidae, Nandidae, and Pristolepidae (with all of which I have very little familiarity).

With regard to the jaws and teeth, those of *Roccus* and *Perca* (without axillary processes) and those of *Lates* and *Pempheris* (with axillary scales) would seem to be very similar and about equally generalized. There appears to be no morphological reason why the jaw structure of any of the four genera should not have developed on the one hand the specializations of *Epinephelus* (without axillary processes) or on the other the peculiarities of *Kyphosus* or *Chaetodon* (with axillary processes). What does seem clear is that the jaw structure of *Epinephelus* could not directly have given rise to that of *Kyphosus*, or vice versa. Therefore it is somewhat disconcerting to find certain families with the jaw specializations of those families with an axillary process to be without such a process. Among such families would appear

TABLE 2
TRENDS OF DEVELOPMENT IN TWO CATEGORIES OF PERCOID FAMILIES

AXILLARY PROCESS PRESENT	AXILLARY PROCESS ABSENT
Narrow-headed fishes, with the eye set well up and back on the head	Broad-headed fishes, with the eye set relatively far forward on the head
Feeding usually accomplished by nipping off or plucking out individual items from their surroundings	Feeding usually accomplished by engulfing whole animals
Carnivores, herbivores, or omnivores	Carnivores
Mouth relatively small	Mouth often large
Jaw teeth often reduced to a single specialized row, conical, incisiform, molariform, or fused	Teeth conical, usually in bands, used for grasping prey
Jaws capable of relatively slight lateral expansion	Jaws capable of relatively great lateral expansion
Maxillary shaft with little rotation when the mouth is opened, forming a supporting cap over the lateral end of the premaxillary	Maxillary shaft with considerable rotation when the mouth is opened, giving slight support to the lateral end of the premaxillary

to be the Sillaginidae (which I have not seen) and the Branchiostegidae (Table 1). No explanation for these apparent anomalies will be attempted here.

The remaining question to be discussed is how Regan's arrangement (1913) of percoid families agrees with other proposed classifications. Since Patterson's views (1964) are much the most radical (see above), they will be considered first. Patterson, as previously noted, has suggested five independent origins for different percoid families. Only one point with regard to these percoid derivations will be added here. Patterson (1964:470, and elsewhere) stressed the primitiveness among percoids of the Scorpidae, Monodactylidae, and Kyphosidae as being "the only perciform families which retain both a toothed endopterygoid and a separate foramen for the hyomandibular trunk of the facial nerve in the lateral wall of the pars jugularis." Although the "primitiveness" of these particular features is not in dispute, it would seem that the dentition and jaw structure of at least *Kyphosus* in the Kyphosidae and of *Microcanthus* in the Scorpidae (Scorpididae) are highly specialized and have evolved a long way from that of *Berycopsis*, from which Patterson would derive them. If, in fact, one were to use jaw structure as a basis for postulating lineages, *Berycopsis* would seem to provide a much more appropriate ancestor for either *Epinephelus* or *Lates* than for *Kyphosus* or *Microcanthus*.

Freihofer (1963) surveyed the various pathways followed by the ramus lateralis accessorius of the facial nerve in teleostean fishes with particular reference to the percoids. These different pathways were then grouped into patterns. Freihofer's Patterns 8, 9, 10, and 13 occur among the percoids, though 13 is restricted to the family Mullidae; it should also be added that a rather large number of species distributed through various percoid families have the ramus lateralis accessorius absent or reduced. An arrangement of percoid families based solely on the patterns worked out by Freihofer would cut across that of Regan (1913), for Patterns 8, 9, and 10 all occur among families with an axillary process and again among families without an axillary process. Thus, the two methods of arrangement would divide percoid families in quite different

ways, although neither one is for that reason necessarily an incorrect indicator of relationships.

The last arrangement of percoid families that will be discussed is that of Matsubara (1955a,b, 1963). Matsubara raises the divisions (superfamilies) of Regan (1913) and of Norman (1957) to subordinal status. But more pertinent to the present discussion, he places the families accepted here as members of the Percoidae under four different suborders. The family Coryphaenidae he places in the Scombrina (equals Scombroidei). The Carangidae, Formiidae, Leiognathidae, Lactariidae, Menidae, and Rachycentridae comprise Matsubara's (1955a:ix) Carangina. The Monodactylidae, Toxotidae, Drepanidae, Ephippidae, Platacidae, Scorpididae, Antigoniidae, Chaetodontidae, Scatophagidae, Zanclidae, and Acanthuridae make up his (Matsubara, 1955b:i) Chaetodontina. In the Percina Matsubara (1955a:ix-x) includes the remainder of the families considered here as percoids, and adds the Cirrhitidae. His serial arrangement of families, though not his groupings, seem to follow rather closely Jordan's (1923) "Classification of Fishes." (Perhaps Matsubara has stated the historical background for his classifications of 1955 and 1963, but both these works are in Japanese and I have been able to get only parts of them translated.) Actually, the relationships of the groups excluded from his Percina have been moot points for a long time (Gregory, 1933). The difficulty, if the carangoids and chaetodontoids are set up as separate groupings from the percoids, is to know what to include in them and on what basis. No two authors are agreed on these matters. If and when carangoid and chaetodontoid groups can be satisfactorily defined, they should undoubtedly be recognized; meanwhile, however, more confusion than clarification would seem to result from such recognition.

SUMMARY AND CONCLUSIONS

The various percoid fishes (Superfamily Percoidae) are considered to represent a single structural theme with numerous variations. There seems no need to consider the group to be of polyphyletic origin, and data on the

supraoccipital crest and on the jaw structure are offered as evidence against certain of Patterson's (1964) specific polyphyletic derivations.

The limits of the superfamily Percoidae adopted by Regan (1913) and Norman (1957) are accepted here, not because they are definitive but because at present they seem to be more concretely based than others yet proposed.

Data on feeding habits, dentition, and jaw structure are brought out in support of an arrangement of percoid families proposed by Regan (1913). That much remains unsatisfactory in this or any other arrangement has been clearly indicated, it is hoped.

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New Monogenetic Trematodes from Hawaiian Fishes, II¹

SATYU YAMAGUTI

IN THIS SECOND REPORT are described seven new species of monogenetic trematodes belonging to six new genera, two of which represent each a new subfamily. One of these two species seems to occur rather uncommonly on the Hawaiian flying fishes; so far I have managed to collect only four specimens after a long search. Although the host of this worm is a pelagic fish, its parasite fauna seems rather endemic in character, inasmuch as the monogenetic and digenetic trematodes found on or in the Hawaiian flying fishes are quite different from those occurring in the allied host species in the neighboring waters. This fact strongly suggests that the distribution of the Hawaiian flying fishes is not very extensive.

All the other new genera of Monogenea to be reported by me from Hawaii will be described in a monograph upon Hawaiian monogenetic trematodes, so that the present report is the last of the series for new Hawaiian monogenetic genera to be described in short articles.

Thanks are due to all the institutions and persons concerned in my survey of Hawaiian trematodes, including the National Science Foundation, the University of Hawaii, my assistant, Mr. Shunya Kamegai, and my wife, Ikuko Yamaguti.

The new species described herein are assigned to the following families and subfamilies:

I. Capsalidae Baird, 1853

Benedeniinae Johnston, 1931

1. *Pseudallobenedenia apharei* n. g., n. sp.
2. *Pseudallobenedenia opakapaka* n. sp.
3. *Lagenivaginopseudobenedenia etelis* n. g., n. sp.

II. Discocotylidae Price, 1936

Opisthogyninae Unnithan, 1962

4. *Metopisthogyne sphyraenae* n. g., n. sp.

III. Pterinotrematidae Bychowsky and Nagibina, 1959

5. *Pseudopterinotrema albulae* n. g., n. sp.

IV. Axinidae Unnithan, 1957

Sibitreminae n. subfam.

6. *Sibitrema poonui* n. g., n. sp.

Cypselurobranchitreminae n. subfam.

7. *Cypselurobranchitrema spilonotopteri* n. g., n. sp.

1. *Pseudallobenedenia apharei* n. gen., n. sp.
Fig. 1

HABITAT: Gills of *Aphareus rutilans*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 45.

DESCRIPTION (based on 21 whole mounts): Body approximately fusiform, 2.6–5.3 mm long, with maximum width of 0.7–1.9 mm at about testicular level. Posterior extremity of body proper attenuated to a flap covering opisthaptor dorsally. Opisthaptor discoid, usually projecting a little beyond posterior end of body proper, 0.43–0.8 mm longitudinally except for scalloped marginal membrane 20–80 μ wide, with a central pit 0.1–0.15 mm in diameter; on the concave ventral surface there are three pairs of anchors, but no definite septa or ridges, although several symmetrical radiating excretory vessels are seen bifurcating or not at their submarginal ends; anterior anchor 28–37 μ long from tip to posterior end, situated posterolateral to central pit; two posterior anchors close together near posterolateral edge of opisthaptor; longer J-shaped medial one slender, 18–33 μ long; shorter lateral one hook-shaped, with bifid root, 14–21 μ long. Prohaptors elliptical, saucer-shaped, 0.54–1.0 \times 0.24–0.48 mm, connected dorsally by medianly incised frontal plate which never projects forward beyond the prohaptors. Mouth opening ventrally at level of posterior end of prohaptors, with one pair or two of eyespots dorsally. Pharynx muscular, incised anteriorly into five lobes, more or less

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ABBREVIATIONS USED IN FIGURES

AB	atrial bulb	GI	genito-intestinal canal	PH	prohaptor
AG	apical gland	GO	Goto's organ	PM	pars muscularis
AP	accessory piece	GP	genital pore	PR	prostatic reservoir
AS	axial sclerite	HC	head cone	RS	receptaculum seminis
BC	bulbus cirri	I	intestine	S	sucker
BE	bulbus ejaculatorius	IB	intestinal branch	SG	shell gland
C	cirrus	ID	intestinal diverticle	T	testis
CA	caudal appendage	LL	larval lappet	TG	terminal genitalia
CL	clamp	M	mouth	U	uterus
CP	cirrus pouch	O	ovary	V	vagina
CS	crown of spines	OC	eyespot	VD	vas deferens
CV	clamp valve	OH	opisthohaptor	VGD	vaginal duct
DE	ductus ejaculatorius	OS	oral sucker	VP	vaginal pore
E	egg	P	pharynx	VR	vitelline reservoir
ES	esophagus	PC	prostatic cell	VT	vitelline gland
GA	genital atrium	PD	prostatic duct	VTD	vitelline duct

constricted laterally near broadly rounded posterior end, $0.22-0.52 \times 0.24-0.65$ mm. Esophagus short; each intestinal limb giving off more or less dendritic outer branches, of which the anterior pair extends into the frontal plate, almost meeting in the median line; posterior-most pair sends out several outer branches reaching lateral edges of body and a few shorter inner branches probably anastomosing each other; no anastomosis between two main intestinal limbs posteriorly.

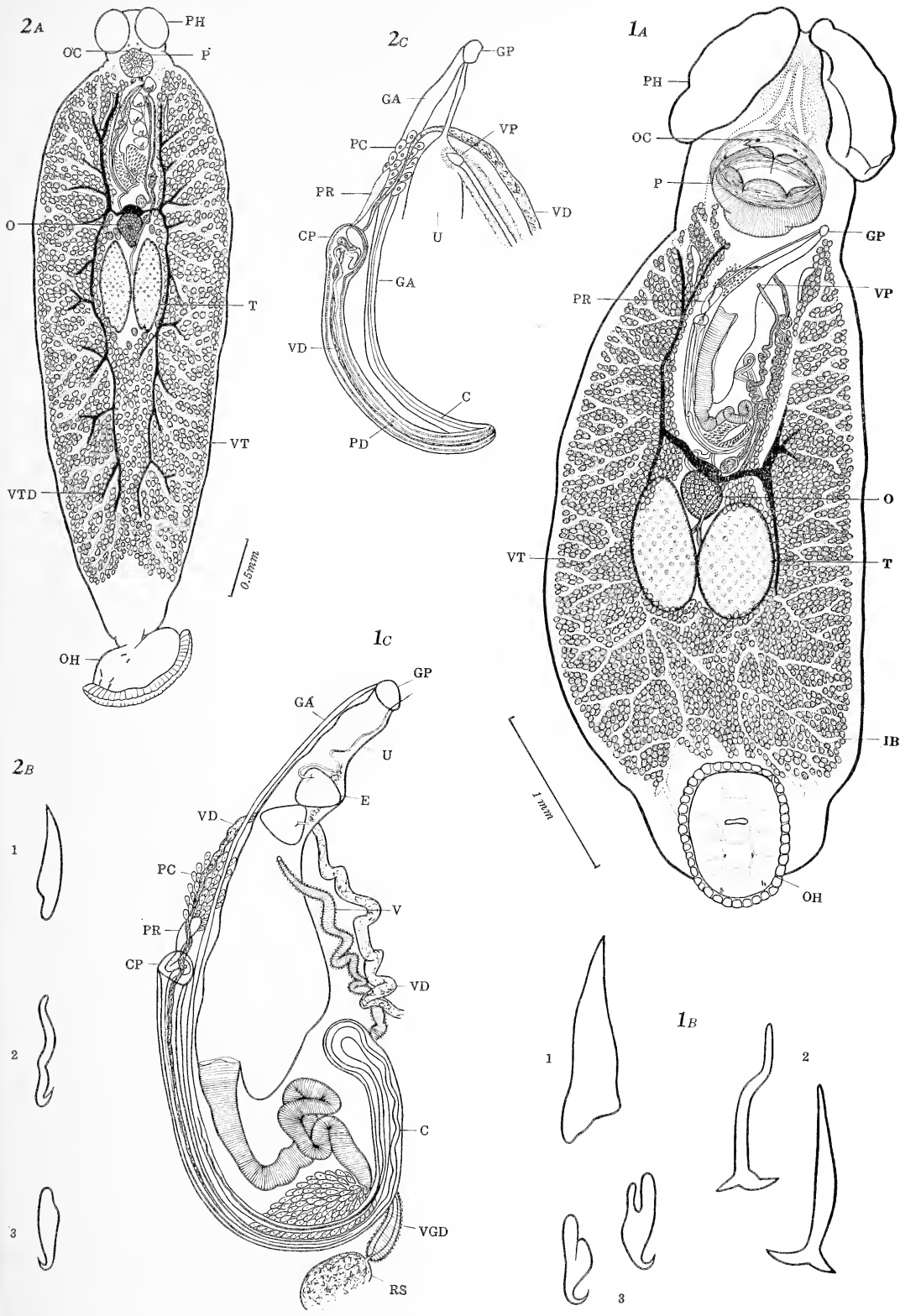
Testes oval to elliptical, $0.28-0.8 \times 0.18-0.5$ mm, directly juxtaposed, largely in posterior part of middle third of body, with paired multinucleate Goto's glands immediately behind. Vas deferens running forward along left margin of ovary, convoluted just medial to left intestinal limb, then crossing uterus dorsally and coming to right side of median line, where it enters the cirrus pouch along with the prostatic reservoir and finally unites with the prostatic duct to lead into extremely long (2-3 mm or more) spicular cirrus. Prostatic cells massed around distal portion of vas deferens and prostatic reservoir which is elliptical, 0.1 mm long by 0.05 mm wide in the type and lies longitudinally alongside the vas deferens. Cirrus pouch somewhat muscular, small (exact length not determinable), containing winding vas deferens

and more or less convoluted prostatic duct; both ducts joining together to form cirrus which is enclosed throughout its length in the thin-walled, tubular, genital atrium, and may or may not project out of the genital pore. The genital atrium is continued from the wall of the cirrus pouch with the same diameter as the latter, but tapers into a very long, narrow tubule which runs backward and then curves toward the left in front of the transverse vitelline duct; it turns back on itself here to follow the same course as its proximal portion, and after passing beside the cirrus pouch proceeds straight obliquely forward to open ventrosublaterally at the level of the posterior end of the pharynx on the left side.

Ovary subglobular, $0.08-0.28 \times 0.1-0.25$ mm, situated medianly between anterior ends of testes. Germiduct arising from anterior end of ovary, joining duct from vitelline reservoir and leading into ootype which passes into a long, winding, muscular uterine duct. Uterus proper forming diverticle-like expansion when distended with eggs; distal portion of uterus proper running obliquely forward along with genital atrium, opening together with latter by a common pore. Shell gland cells developed around ootype. Eggs mostly rounded conical, but rounded triangular in flattened condition,

FIG. 1. *Pseudallobenedenia apharei* n. g., n. sp. 1A, Holotype, ventral view; 1B, haptoral anchors of paratype; 1C, terminal genitalia of paratype, ventral view.

FIG. 2. *Pseudallobenedenia opakapaka* n. sp. 2A, Holotype, ventral view; 2B, haptoral anchors; 2C, terminal genitalia, ventral view.



with extremely long, very fine, antipolar filament at base, $0.1-0.125 \times 0.09-0.115$ mm as measured in life and in lactophenolglycerin jelly. Vitelline follicles extending in lateral fields from level of posterior part or end of pharynx to base of posterior flap covering opisthohaptor, confluent in median line between testes and opisthohaptor, intruding into small area between transverse vitelline ducts and testes; transverse vitelline ducts united medially, forming inconspicuous vitelline reservoir only $20-110\mu$ anteroposteriorly. Vagina opening ventral to uterus by a very small pore a little behind intestinal bifurcation; vaginal duct winding along with vas deferens medial to left intestinal limb; receptaculum seminis vaginae oval, $50-150 \times 30-110\mu$, lying between left transverse vitelline duct and ootype; seminal duct connecting seminal receptacle with vitelline reservoir very short. Excretory vesicle funnel-shaped, symmetrical, opening dorsally at level of intestinal bifurcation.

DISCUSSION: This genus very closely resembles *Allobenedenia* Yamaguti, 1963 in gross anatomy, but differs in minor details as shown in Table 1.

The present species differs from *P. opakapaka* to be described below in that the genital atrium

is much longer, often convoluted, and contains an extremely long cirrus. The unusually long and wide uterus in *P. aphareis* is worth noting.

2. *Pseudallobenedenia opakapaka* n. sp.

Fig. 2

HABITAT: Gills of *Pristipomoides microlepis* (local name "opakapaka"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 46.

DESCRIPTION (based on three whole mounts): Body elongate, distinctly constricted immediately behind prohaptor, $3.0-5.5$ mm in total length including opisthohaptor, with maximum width of $0.1-0.15$ mm at level of testes. Opisthohaptor bell-shaped, $0.6-0.8$ mm in transverse diameter, provided with a scalloped marginal membrane. There are three submedian pairs of weakly developed anchors on the inner surface of the posterior half of the opisthohaptor; anterior anchor rod-shaped, $40-50\mu$ long, middle and posterior anchors a little apart from the anterior, close together near haptoral margin; middle one somewhat undulating, barbed distally, $40-43\mu$ long; posterior one hook-shaped, $18-25\mu$ long. Prohaptor oval, saucer-shaped, glandular, $0.21-0.28$ mm long; between the two haptors is seen the truncate head end level with the anterior end of the haptor. Two pairs of eyespots anterodorsal to pharynx. Pharynx subglobular, without constriction, $42-58 \times 52-62\mu$. Esophagus very short, surrounded on each side by postpharyngeal cells, whose ducts appear to open into the pharyngeal lumen close to its posterior end. Intestinal limbs with comparatively long, subdivided, outer branches, terminating separately a short distance away from posterior end of body.

Testes elliptical, juxtaposed at anterior part of middle third of body, $0.37-0.7 \times 0.17-0.28$ mm, with paired Goto's glands immediately behind. Multinucleate organs like Goto's were found immediately in front of the testes and beside ovary. Vas deferens convoluted between left intestinal limb and shell gland complex, then forming a very long horseshoe-shaped loop across uterus and cirrus pouch dorsally, penetrating cirrus pouch at its anterior base, finally joining prostatic duct at posterior end of cirrus pouch. Cirrus pouch cylindrical, $0.2-0.7$ mm

TABLE 1
DIFFERENTIATION OF *Pseudallobenedenia*
FROM *Allobenedenia*

CHARACTER	<i>Allobenedenia</i>	<i>Pseudallobenedenia</i>
Frontal hood	present	absent
Cirrus	long	extremely long
Genital atrium	not extremely long	extremely long, convoluted or straight
Vaginal opening	marginal or submarginal, prebifurcal	submedian, postbifurcal
Receptaculum seminis	absent	well developed
Vitelline reservoir	saccular, very distinct	no definite reservoir

long, arcuate, strongly muscular, swollen at its forwardly directed base, situated longitudinally between right intestinal limb and uterus, containing prostatic duct and vas deferens, both of which are straight, narrow, and close together, though convoluted at the anterior base of the cirrus pouch. Cirrus spicular, long, enclosed in sheathlike genital atrium which extends from the posterior distal end of the cirrus pouch to the genital pore along the dorsal side of the cirrus pouch. This overlapping portion is shown separately in the figure. Prostatic reservoir elongate, $80-90 \times 100-130\mu$, situated immediately in front of base of cirrus pouch. Genital pore common, just posterosinistral to pharynx.

Ovary subglobular, $0.17-0.27 \times 0.17-0.22$ mm, situated between two testes and vitelline reservoir. Shell gland complex strongly developed. Uterus distended with eggs. Eggs rounded pyramidal, with triangular base in balsam mounts, $0.12-0.14 \times 0.12-0.15$ mm in life, with very fine, long filament at one basal corner. Vagina opening ventrally in left submedian line a little posterior to intestinal bifurcation; vaginal duct thick-walled, running straight backward and opening into oval seminal receptacle which measures 100μ by 80μ in the type. Vitellaria coextensive with intestinal limbs and their branches; vitelline reservoir transversely elongated, not forming a compact mass, $60-90\mu$ anteroposteriorly. Paired excretory vesicles conspicuous at level of uterus.

DISCUSSION: The differences between this species and the type species are given in the discussion of the type species.

Pseudallobenedenia n. gen.

GENERIC DIAGNOSIS: Capsalidae, Benedeniinae. Opisthohaptor discoid, not septate, with scalloped marginal membrane, armed with three pairs of anchors. Prohaptors not enclosed in hoodlike frontal plate. Pharynx muscular, lobed anteriorly; intestinal limbs branched, not confluent posteriorly, though their posterior inner branches may anastomose. Testes juxtaposed; vas deferens convoluted medial to left intestinal limb. Prostatic cells and reservoir outside cirrus pouch. Cirrus pouch long; cirrus extremely long, enclosed in extremely long, tubular, genital atrium. Genital pore common, sublateral or sub-

median, level with posterior end of pharynx or farther behind. Ovary immediately pretesticular. Eggs rounded conical or pyramidal, with very long filament at base or basal corner. Vitellaria extensive; vitelline reservoir inconspicuous. Vagina opening submedianly ventral to uterus at postbifurcal level; receptaculum seminis vaginae well developed. Gill parasites of marine teleosts.

TYPE SPECIES: *P. apharei* n. sp., on *Aphareus rutilans*; Hawaii.

OTHER SPECIES: *P. opakapaka* n. sp., on *Pristipomoides microlepis*; Hawaii.

3. *Lagenivaginopseudobenedenia etelis*

n. g., n. sp.

Fig. 3

HABITAT: Gills of *Etelis carbunculus* (local name "onaga"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 47.

DESCRIPTION (based on three whole mounts): Body elliptical, flat, 2.9–4.3 mm in total length, 1.8–2.3 mm wide in midregion; head and neck region contracted and well separated from trunk. Opisthohaptor elliptical, 0.53–0.75 mm long, with finely scalloped marginal membrane 30–70 μ wide and three pairs of anchors; number of marginal hooklets not determined; anterior anchor 0.13–0.17 mm long, sharp-pointed anteriorly, nonalate, with two small blunt stumpy processes of unequal length at posterior end; middle and posterior anchors definitely smaller than anterior; middle one slender, 50–80 μ long, with undulating root and minute terminal claw; posterior one enlarged and flattened from side to side basally, 30–40 μ long, terminating in a minute claw. Prohaptors saucer-shaped, paired, close together, $0.19-0.23 \times 0.36-0.42$ mm, containing glandular tissue which extends not only backward but also inward to be confluent in the median line posterior to somewhat incised frontal margin. Two pairs of eyespots present anterodorsal to pharynx. Pharynx spherical, $0.27-0.29 \times 0.3-0.31$ mm, glandular rather than muscular, papillate internally. Esophagus practically absent; ceca with numerous dendritic outer branches, not confluent posteriorly.

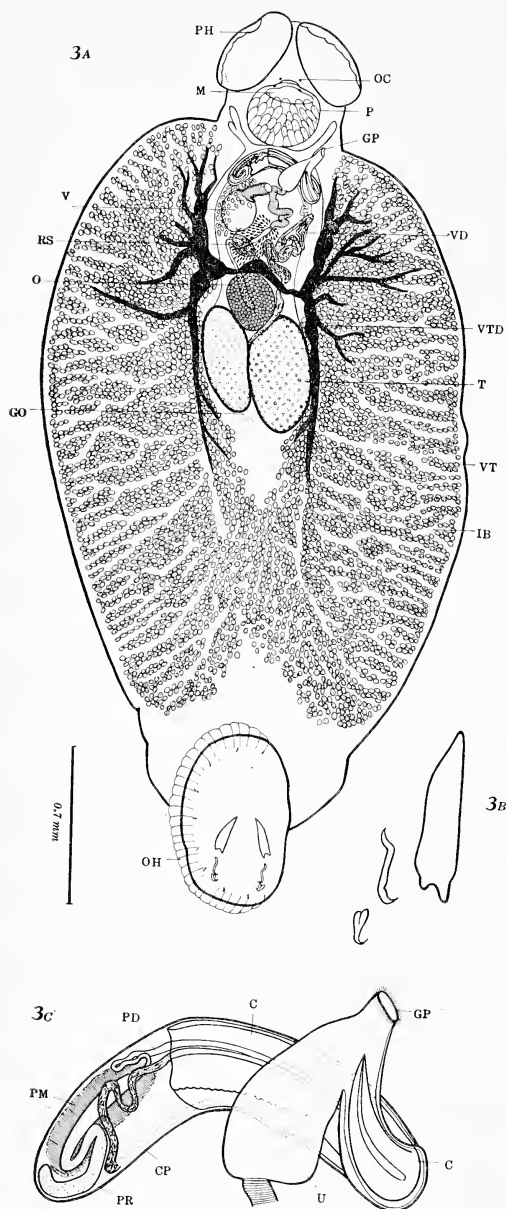


FIG. 3. *Lagenivaginopsendobenedenia etelis* n. g., n. sp. 3A, Holotype, ventral view; 3B, haptoral anchors of holotype; 3C, terminal genitalia of holotype, ventral view.

Testes elliptical, $0.31-0.5 \times 0.2-0.34$ mm, juxtaposed contiguously at anterior part of middle third of body. Rudimentary Goto's organ present. Vas deferens convoluted immediately anterosinistral to vitelline reservoir, then winding along posterior wall of cirrus pouch, which

it penetrates from the dorsal side; after entering the cirrus pouch it pursues a short winding course, then a long straight course alongside the distal portion of the prostatic duct, with which it finally unites to form the ejaculatory duct. Cirrus pouch subcylindrical, thin-walled, $0.25-0.4 \times 0.08-0.1$ mm, curved transversely behind pharynx, containing at its base a small, tubular, prostatic reservoir and cylindrical pars muscularis of prostatic duct which is $0.1-0.13$ mm long and provided with a thick coat ($30-60\mu$ wide) of fine circular muscle fibers. Prostatic cells distributed around base of cirrus pouch. Cirrus elongate conical, pointed, 0.42×0.06 mm in the type; it may or may not project out of the genital pore. Common genital pore posterosinistral to pharynx, a little (0.1 mm in the type) away from nearly right angle formed by neck and trunk.

Ovary subglobular to oval, $0.15-0.3 \times 0.09-0.22$ mm, situated medianly, with its posterior end intercalated between two testes. Ootype spherical, $0.15-0.2$ mm in diameter, provided with epithelial lining; uterus proper well separated from ootype, 0.2 mm wide in the type, opening into common genital pore by a funnel-shaped passage. No eggs observed. Vitellaria consisting of small follicles, coextensive with intestine, wide apart anteriorly, but confluent posteriorly; paired longitudinal collecting ducts distended with yolk cells; transverse duct may be narrower, up to 70μ wide in the larger paratype, not forming a definite reservoir. Vagina lageniform, 0.17 mm wide in the type, muscular at its narrow neck, situated between uterus and right intestinal limb, opening almost midventrally behind cirrus pouch. Seminal receptacle oval, 0.1×0.055 mm in the type, between vagina and vitelline reservoir. Excretory system not made out.

DISCUSSION: This genus, characterized by the head and neck being marked off from the trunk and by the peculiar structure and position of the vagina, bears a certain resemblance to *Pseudobenedenia* Johnston, 1931, especially in the prostatic vesicle being enclosed in the cirrus pouch, but it seems justified to separate the genus in question from *Pseudobenedenia* on the basis of the above mentioned features. The compound generic name refers to the lageniform vagina and close relationship to *Pseudobenedenia*.

Lagenivaginopseudobenedenia n. g.

GENERIC DIAGNOSIS: Capsalidae, Benedeniinae. Prohaptors consisting of paired glandular saucers placed close together. Opisthohaptor discoid, aseptate, with scalloped marginal membrane, armed with three pairs of anchors. Eyespots present. Head and neck region much narrower than trunk and well marked off from it. Pharynx spherical, without constriction, rather glandular, papillate internally. Intestinal limbs with dendritic outer branches, not confluent posteriorly. Testes juxtaposed, entire. Vas deferens strongly convoluted in front of left transverse vitelline duct, passing transversely behind cirrus pouch and penetrating it near its base. Cirrus pouch cylindrical, extending transversely behind pharynx, containing small prostatic reservoir and well developed pars muscularis of prostatic duct at its base. Cirrus elongate conical, pointed, projecting into thin-walled genital atrium. Common genital pore ventrosubmedian, well apart from body margin. Ovary entire, not separated from testes by vitellaria. Vitellaria co-extensive with intestine; no definite vitelline reservoir. Vagina lageniform, between uterus and right intestinal limb, opening almost mid-ventrally behind cirrus pouch; seminal receptacle well developed. Gill parasites of marine teleosts.

TYPE SPECIES: *L. etelis* n. sp., on *Etelis carbunculus*; Hawaii.

4. *Metopisthogyne sphyraenae* n. gen., n. sp.
Fig. 4

HABITAT: Gills of *Sphyraena helleri* (local name "kawalea"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 48.

DESCRIPTION (based on five whole mounts): Body 4.4–8.9 mm long, slender, gradually widened toward opisthohaptor which is 0.8–2.0 mm long by 0.6–1.0 mm wide at base and bears four pairs of short-stalked clamps and a short, trapezoidal, median, caudal lappet provided with three pairs of hooks. Clamp skeleton 0.24–0.3 mm in transverse diameter, consisting of a very stout median spring, a pair of inner basal sclerites, two pairs of arcuate lateral sclerites and a pair of accessory sclerites; one prong

of median spring with three or four minute holes, enlarged at apex in form of a triangle; other prong with anchor-shaped apex, may be bulbously swollen near its base. Of the caudal hooks the larger outermost is 41–46 μ long from tip of root to height of curve of blade, and has a curved guard a little shorter than root; the smallest middle is 16–18 μ long and has a comparatively long root and a short curved blade; the innermost is somewhat similar in shape to the outermost and 25–28 μ long. Head rounded in front, 0.16–0.32 mm wide, with ventral mouth aperture and a pair of groups of gland ducts at apex; paired oral suckers aseptate, muscular, 70–93 \times 58–72 μ , close together, followed by ovoid nonmuscular pharynx 51–70 μ long by 48–58 μ wide; esophagus 1.0–2.0 mm long, simple, wide, bifurcating just in front of vaginal pore; intestinal limbs with short side branches, terminating separately, one at base of opisthohaptor and the other a little more posteriorly.

Testes small, ovoid, 93–162 in total number, extending in interintestinal field from anterior part of middle third of body to anterior half of caudal third, mostly preovarian, partly para- and postovarian. Vas deferens strongly winding in median field between testes and vagina; in the region between the vagina and the pars muscularis there are numerous prostate cells, though the pars prostatica is not distinctly differentiated. Pars muscularis representing ejaculatory duct, 0.35–0.45 mm long by 40–60 μ wide, provided with strong transverse or spiral muscle fibers, followed by muscular cirrus 0.18–0.26 mm long which is bulbously swollen near its distal end and projects into the nonmuscular genital atrium in the type. Genital atrium opening on left margin of body at a distance of 0.55–0.8 mm from head end.

Ovary tubular, long, folded back on itself just medial to left intestinal limb, 0.3–0.4 mm long lineally as a whole, arising about one-third of body length from posterior extremity. Germiduct giving rise to genito-intestinal duct before joining vitelline reservoir. This duct opens into the left intestinal limb a little anterior to the distal end of the ovary. Uterus midventral, containing only one fusiform egg in the type. Eggs 0.17–0.18 mm long, with rigid bipolar filaments 0.15–0.21 mm long. Vitellaria largely

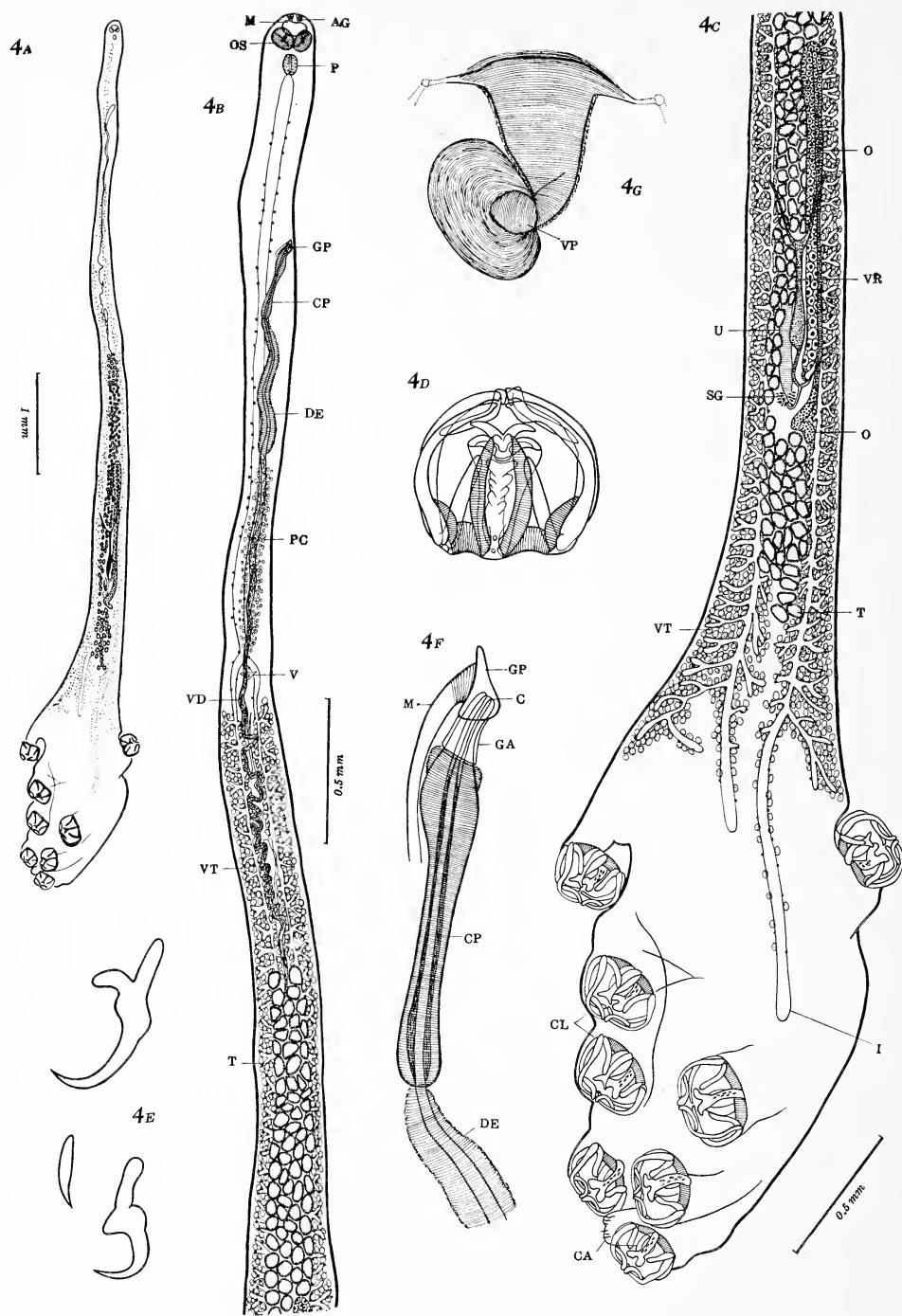


FIG. 4. *Metopishogyne sphyraenae* n. g., n. sp. 4A, Holotype, ventral view; 4B and 4C, enlarged anterior and posterior regions of holotype, ventral view; 4D, clamp of paratype; 4E, anchors on caudal appendage of paratype; 4F, terminal genitalia of holotype, ventral view; 4G, vagina of paratype, ventral view.

coextensive with intestine, commencing a little behind vaginal pore and terminating at base of opisthohaptor; vitelline reservoir Y-shaped, in ovarian zone. Vagina funnel-shaped, strongly muscular, sending out a short narrow duct on each side of its anterior end. This duct appears to be connected with the anterior end of the longitudinal vitelline duct of its own side, although no distinct connecting duct is seen. Vaginal pore middorsal, postbifurcal, provided with a conspicuous bulb of fine lamellar muscle fibers, situated at a distance of 1.2–2.25 mm from head end.

DISCUSSION: This genus differs markedly from *Opisthogyne* Unnithan, 1962, in the distribution of the testes. In *Opisthogyne* the testes are limited to the preovarian region, whereas in the present genus they are much more numerous and more extensive. The V-shaped ridges characteristic of *Opisthogyne* and *Gemmacaputia* Tripathi, 1959, are absent in the posterior part of the body in the present genus.

Metopisthogyne n. gen.

GENERIC DIAGNOSIS: Discocotylidae, Opisthogyninae. Body symmetrical, elongate, without V-shaped ridges posteriorly. Four pairs of similar clamps of *Gastrocotyle* type. Terminal lappet with three pairs of hooks. Esophagus long; intestine with side branches, terminating separately. Testes numerous, mainly preovarian, partly para- and postovarian. Ductus ejaculatorius strongly muscular. Cirrus muscular, unarmed. Genital pore ventromarginal. Ovary tubular, folded back on itself in posterior half of body; eggs fusiform, with filament at each pole. Vitellaria coextensive with intestine. Vaginal pore middorsal, immediately postbifurcal. Gill parasites of marine teleosts.

TYPE SPECIES: *M. sphyraenae* n. sp., on *Sphyraena helleri*; Hawaii.

5. *Pseudopteriotrema albulae* n. g., n. sp. Fig. 5

HABITAT: Gills of *Albula vulpes*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 49.

DESCRIPTION (based on 26 whole mounts): Body slender, cylindrical, 1.75–2.4 mm in

length exclusive of haptor clamps, up to 4.5 mm in length including clamps, 0.12–0.26 mm wide in ovariostesticular region. Opisthohaptor fan-shaped, asymmetrical, on posterior extension of body proper, with nine pedunculate clamps. As numbered from the right end of the opisthohaptor of the type the first to the ninth clamp gave the following measurements, presenting different features respectively:

(1) First clamp 0.18 mm long, divided into a caudal appendage bearing a pair of large subapical anchors 37–48 μ long and two more, very small, apical hooklets 9–15 μ long, and a shorter clamp than others. This clamp consists of two opposing valves fringed on each side with about a dozen curved spines and supported by comparatively short stout sclerites.

(2) Second clamp arising from common trunk with first, 0.25 mm long, consisting of a slender stalk about 0.2 mm long, and provided on each side with membranous fringe supported by a row of about a dozen acicular spines and a single axial sclerite; apical clamp valve single, fringed with over a dozen curved spines.

(3) Third clamp about 0.4 mm long from its basal two-valved sucker to tip of double terminal clamp valve; its stalk supported by two unequal axial sclerites, one of which articulates with the sclerite of the second clamp at the base, while the other slender one articulates with the stronger axial sclerite of the fourth clamp; axial clamp valves pressed against each other.

(4) Fourth clamp 0.38 mm long, similar in structure to the third, with double apical clamp valve, bearing at base a two-valved sucker on the right and a larval lappet on the left. This lappet is a plump rod-shaped lobe 25–40 μ long by 15–22 μ wide and bears two pairs of very small larval anchors 12–17 μ long.

(5) Fifth clamp 0.47 mm long from its basal sucker to apex which consists of two similar valves.

(6) Sixth clamp 0.25 mm long, with double apical valve similar in structure to that of third.

(7) Seventh clamp 0.23 mm long; terminal clamp valves symmetrical.

(8) Eighth clamp about 0.18 mm long, with two separate apical valves and a common stalk supported by two parallel axial sclerites, of

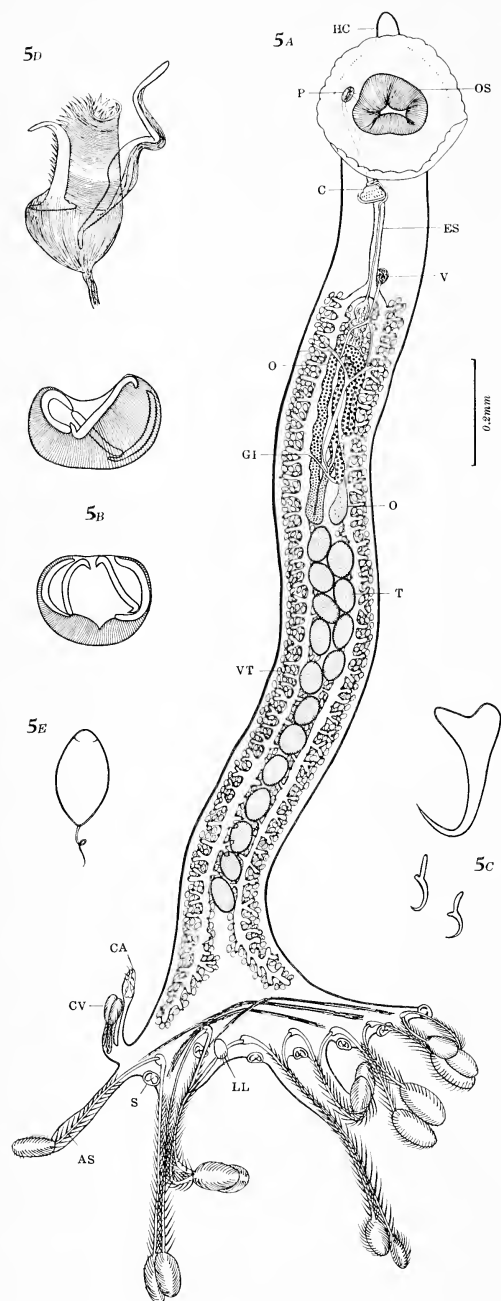


FIG. 5. *Pseudopteriotrema alubulae* n. g., n. sp. 5A, Holotype, ventral view; 5B, two-valved sucker; 5C, anchors on caudal appendage of holotype; 5D, cirrus and its accessory sclerites of paratype, dorsal view; 5E, egg.

which the right one articulates with the left axial sclerite of the seventh clamp and the left one articulates with the extreme left ninth sclerite.

(9) Ninth clamp about 0.12 mm long and fringed on each side with a row of spines like other clamp stalks, but bears one apical clamp valve, although it has a two-valved sucker on the left side of its base.

The above mentioned two-valved suckers, 23–40 μ wide and seven in all, are arranged in a transverse row at the base of the clamps. Each sucker has a sclerotized frame consisting of four sclerites and appears ∞ -shaped in profile.

Prohaptor circular, 0.2–0.47 mm in diameter, membranous, with somewhat crenulated margin and a simple middorsal cone 40–70 μ long and 40–70 μ wide at base. Oral sucker 0.11–0.21 mm in diameter, opening at bottom of prohaptor; prepharynx present; pharynx always lateral to oral sucker, cylindrical, 40–60 \times 20–30 μ ; esophagus very narrow, 0.3–0.65 mm long. Ceca with short branches, terminating separately at base of opisthohaptor.

Testes rounded, up to 25 in number (mostly 16), arranged in a zigzag longitudinal row, occupying greater part of postovarian interintestinal field. Vas deferens may be strongly swollen in preovarian interintestinal field. Cirrus plug-shaped, muscular, covered inside with spinules, 50–90 \times 27–50 μ , with two unequal sclerotized filaments at base; anterior filament 50–120 μ long, usually widened distally, posterior hook-shaped, 35–60 μ long, both often appressed against cirrus. Genital pore ventro-medial, 0.06–0.22 mm posterior to pharynx.

Ovary turned back on itself five times, forming N-shaped loop posteriorly and double loop anteriorly, situated in anterior part of middle third of body. The germiduct running forward gives off the genito-intestinal duct near its origin and soon unites with the descending vitelline stem. Uterus largely ventromedial; eggs elliptical, 110–130 \times 50–75 μ , with long, very fine filament at antipercular pole. Vitellaria coextensive with intestinal limbs; vitelline reservoir Y-shaped, with long, sometimes short, stem, and rather short arms, coinciding with ovary. Vagina well cuticularized, with wide mid-

dorsal opening 0.1–0.35 mm posterior to genital pore, usually anterior to anterior end of vitellaria, but sometimes much posterior to this level. Vaginal duct inverted Y-shaped, each branch opening into arm of vitelline reservoir of its own side.

DISCUSSION: This genus bears a superficial resemblance to *Pterinotrema* Caballero, Bravo-Hollis, and Grocott, 1954, but differs from it fundamentally in the structure of the clamps and the terminal genitalia, and in possessing a typical oral sucker and a pharynx. I prefer to separate it as representing a new genus, for which the name *Pseudopterinotrema* is suggested, with the following diagnosis.

Pseudopterinotrema n. g.

GENERIC DIAGNOSIS: Pterinotrematidae. Body small, cylindrical. Prohaptor circular, with a dorsal conical papilla. Opisthohaptor with nine long-stalked clamps, one of which, to the extreme right in the type, bears an armed caudal appendage. Each clamp, except for two extreme right ones, with two axial sclerites fringed with spines on its stalk, and two terminal clamp valves which are also fringed with spinelets. A transverse row of six small, two-valved suckers present at base of third to seventh clamp stalks, extreme left one to left of base of ninth sclerite. At base of fourth clamp is a rod-shaped lobe bearing two pairs of very small larval hooklets. Oral sucker and pharynx present. Intestinal limbs with short outer branches, terminating separately at base of opisthohaptor. A number of rounded testes in a zigzag longitudinal row in posterior interintestinal field. Copulatory organ consisting of plug-shaped, muscular, spined cirrus and two accessory sclerites. Genital pore ventromedian, immediately behind prohaptor. Ovary tubular, looped, pretesticular. Vagina sclerotized, opening middorsally near intestinal bifurcation; vaginal duct inverted Y-shaped, each branch connected with arm of vitelline reservoir of its own side. Eggs elliptical, filamented at antioepicardic pole. Vitellaria coextensive with intestine. Gill parasites of marine teleosts.

TYPE SPECIES: *P. albulae* n. sp., on *Albula vulpes*; Hawaii.

6. *Sibitrema poonui* n. g., n. sp.

Fig. 6

HABITAT: Gills of *Parathunnus sibi* (local name "poonui"); Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 50.

DESCRIPTION (based on a single gravid specimen): Body 19.2 mm in total length, distinctly divided into three regions: body proper, haptor stalk, and haptor region. Body proper slender, lanceolate, tapered anteriorly, with a pair of compact eyespots, constricted behind, 11.7 mm long, 1.4 mm wide in posterior part where the ovary is situated; haptor stalk fusiform, 4.3×0.45 mm, containing intestine and vitelline gland alone, attenuated posteriorly and then gradually enlarged to pass into haptor region which is spatulate, produced posteriorly into a conical terminal appendage. This appendage is 0.2 mm long, 0.2 mm wide at the base, and bears on the ventral surface of its apex two pairs of larval hooklets of different size; outer pair 46μ long, inner pair 21μ long, both with a very prominent guard and a well curved blade. On the left border of the haptor region is a single longitudinal row (about 3 mm long) of 48 clamps $50\text{--}90\mu$ in transverse diameter. Clamp skeleton consisting of a pair of inner basal processes, two pairs of lateral arms, a pair of accessory pieces meeting in median line, and a stout median spring, one end of which is anchor-shaped, while the other end is surmounted by a Y-shaped apical piece. Mouth cavity wide, opening ventroterminally, with oval paired suckers ($46 \times 23\mu$) laterally and a globular, weakly muscular, median pharynx at its bottom; esophagus simple, 1.45 mm long, contracted at beginning, but soon enlarged to width of 0.15 mm, bifurcating immediately behind genital pore. Intestinal limbs with numerous short inner and longer outer branches; right limb terminating at base of terminal appendage, left one 0.5 mm farther in front.

Testes rounded, 75 in total number, pre-, para-, and postovarian; preovarian testes in two parallel submedian rows of 15 or 16 each; parovarian testes 18 or 19, in two longitudinal rows immediately outside ovarian loop; behind the ovary there are only several testes in the median field. Vas deferens median, dorsal to uterus;

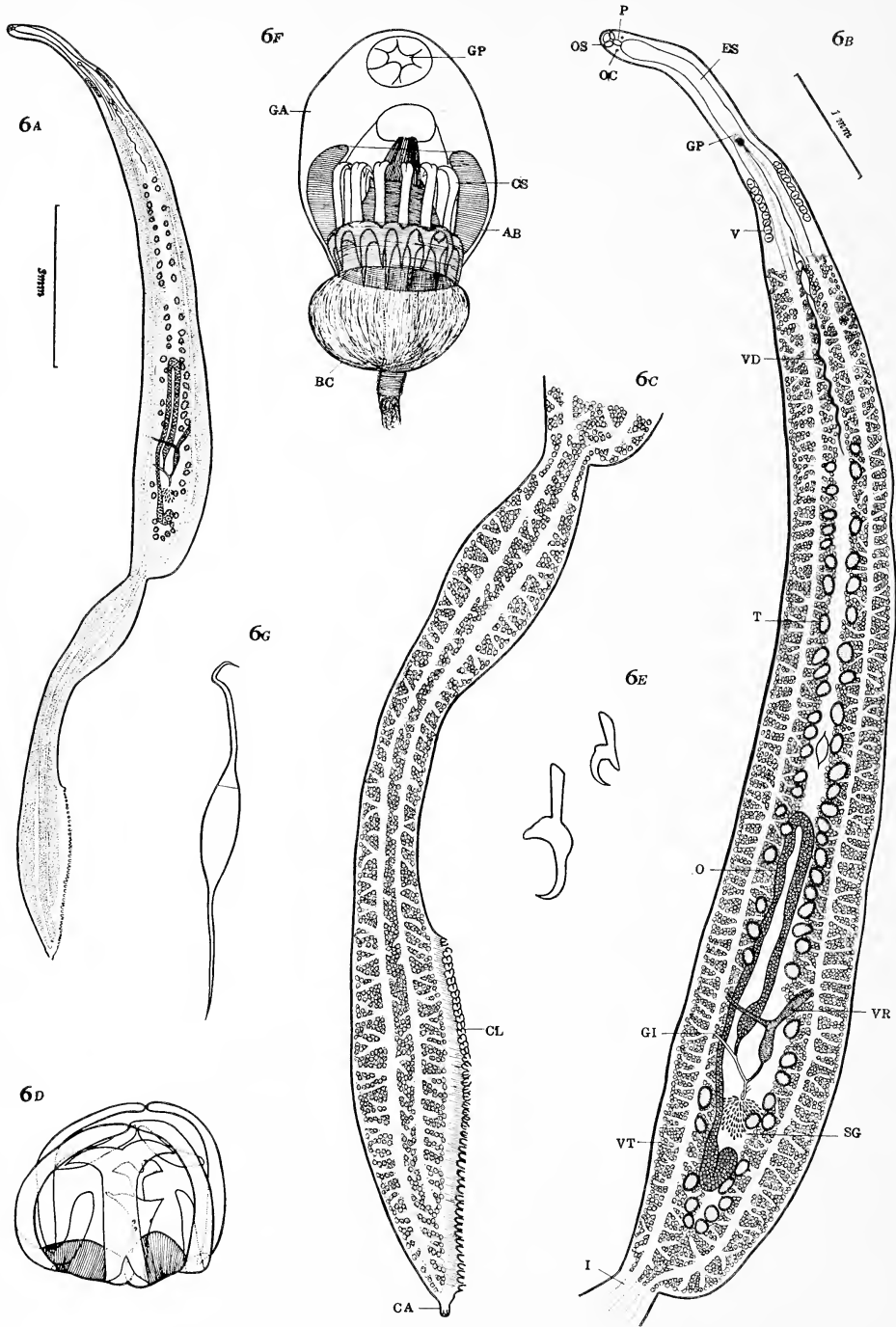


FIG. 6. *Sibitrema poonui* n. g., n. sp. 6A, Holotype, ventral view; 6B and 6C, enlarged anterior and posterior regions of holotype, ventral view; 6D, clamp; 6E, anchors on caudal appendage of holotype; 6F, terminal genitalia of paratype, dorsal view; 6G, egg.

bulbus cirri weakly muscular, 70μ in diameter, situated just ventral to intestinal bifurcation. Cirrus consisting of several sharp-pointed spines which are 35μ long and bundled together immediately in front of atrial crown of 12 spines; these spines are $51\text{--}56\mu$ in length including base which forms a ring of 12 backwardly directed prongs; the shaft of each spine is straight, but the apex is curved inward and bifid at the tip. This crown of spines is enclosed in a very thick-walled atrial bulb of radial muscle fibers, which in turn is enclosed in a membranous genital atrium. Genital pore midventral, at anterior end of genital atrium, 1.45 mm from head end.

Ovary tubular, bent back on itself on right side of median line, 3.15 mm long as a whole, swollen (0.3 mm wide) at postequatorial proximal end in form of a recurved mass and at distal end in form of a club, from the posterior end of which the germiduct arises. Genito-intestinal canal arising from near middle of germiduct, running obliquely forward across proximal portion of ovary ventrally to empty into right intestinal limb. Vitelline follicles small, coextensive with intestinal branches, commencing a little behind vaginae; vitelline reservoir Y-shaped, to left of distal end of ovary, connected with germiduct by a narrow descending median stem 0.15 mm long. Uterus straight, midventral, containing a few eggs; eggs fusiform, $0.23\text{--}0.25 \times 0.07\text{--}0.09$ mm, with filament $40\text{--}60\mu$ long at each pole. Vaginae symmetrical, about 0.5 mm long, divided into a series of several (8–14) areolae, situated laterally about halfway between genital pore and anterior end of vitellaria.

DISCUSSION: This genus closely resembles *Allospseudaxine* Yamaguti, 1943, in internal anatomy, but differs markedly in general body shape and, what is more important, in the structure of the clamp. On the basis of the latter difference I prefer to propose the new subfamily Sibitrematinae for its reception, with the following diagnosis.

Sibitrematinae n. subf.

SUBFAMILY DIAGNOSIS: Axinidae. Body divided into three distinct regions. Opisthohaptor asymmetrical, without prehaptoral larval

anchors. Clamp skeleton consisting of two pairs of lateral sclerites, one pair of basal inner sclerites, an arcuate median spring, and a pair of accessory sclerites. A terminal lappet bearing larval hooklets present. Testes numerous, pre-, para-, and postovarian. Ovary inverted U-shaped. Vaginae double, symmetrical.

Sibitrema n. g.

GENERIC DIAGNOSIS: Axinidae, Sibitrematinae. Body long, divided into three distinct regions: body proper, haptoral stalk, and opisthohaptor with a row of numerous clamps unilaterally and a terminal lappet bearing two pairs of anchors. Paired oral suckers poorly developed. Esophagus bifurcating near genital pore. Intestinal limbs with numerous side branches, terminating blindly near base of terminal lappet. Testes numerous, pre-, para-, and postovarian. Genital atrium membranous, immediately prebifurcal, enclosing atrial bulb of radial muscle fibers at bottom, latter in turn provided inside with a crown of spines, beyond which the bundled cirrus spines project forward. Ovary tubular, bent back on itself in middle third of body. Genito-intestinal canal crossing proximal portion of ovary. Eggs with filament at each pole. Vitellaria coextensive with intestinal branches; vitelline reservoir Y-shaped, in ovarian region. Vaginae divided into a series of several areolae, situated about halfway between genital pore and anterior end of vitellaria. Gill parasites of marine teleosts.

TYPE SPECIES: *S. poonui* n. sp., on *Parathunnus sibi*; Hawaii.

7. *Cypselurobranchitrema spilonopteris* n. g., n. sp.

Fig. 7

HABITAT: Gills of *Cypselurus spilonopteris*; Hawaii.

HOLOTYPE: U. S. Nat. Mus. Helm. Coll., S. Y. No. 51.

DESCRIPTION (based on four whole mounts): Body 7–10 mm in total length, enlarged laterally up to 2.3–3.5 mm wide in midregion; anterior third abruptly tapered toward head end which is 0.2–0.4 mm wide at the level of the oral suckers; posterior third occupied by large

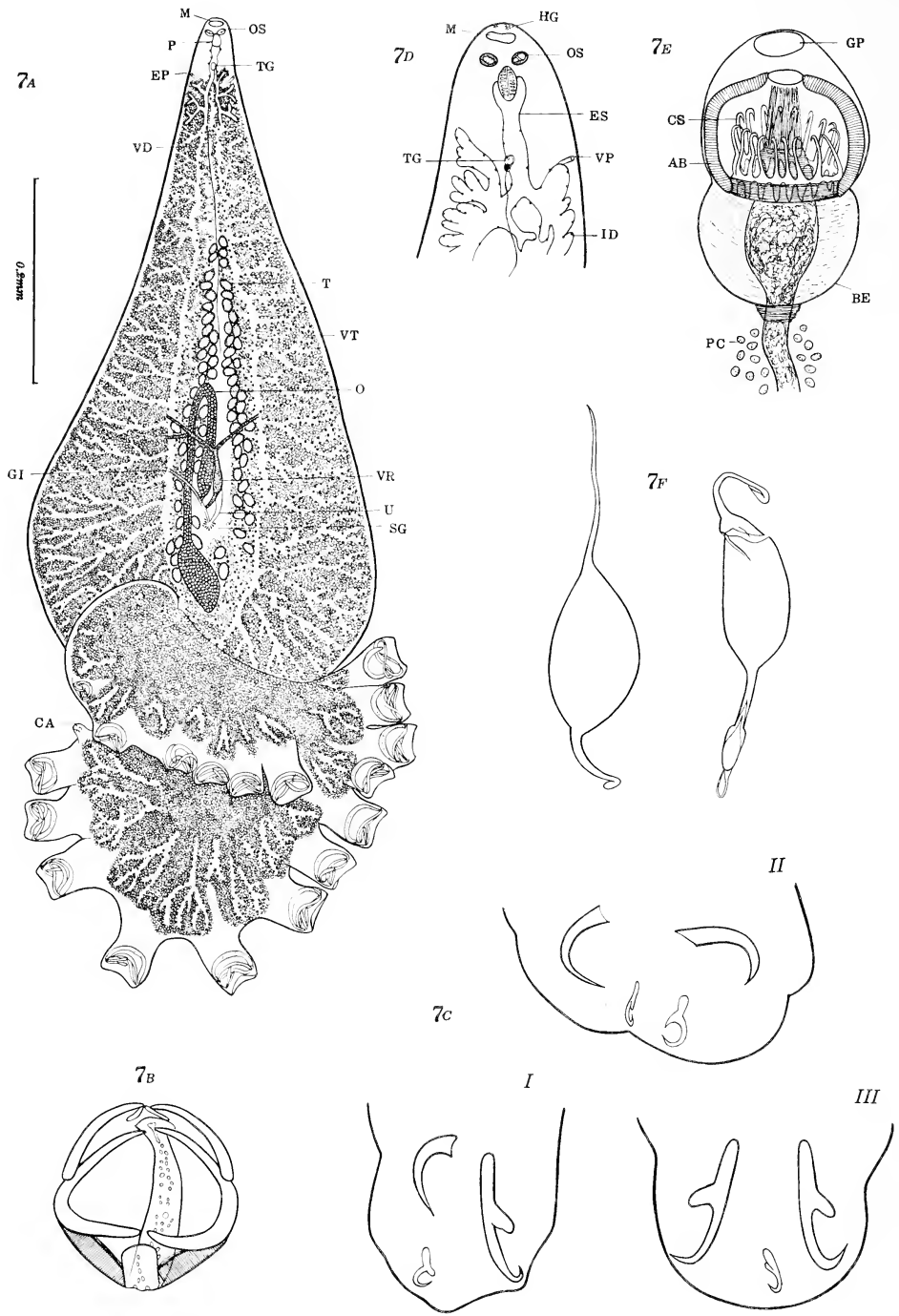


FIG. 7. *Cypselurobranchitrema spilonotopteri* n. g., n. sp. 7A, Holotype, ventral view; 7B, clamp; 7C, anchors on caudal appendage of holotype (I) and two paratypes (II and III); 7D, anterior extremity of paratype, ventral view; 7E, terminal genitalia of paratype, ventral view; 7F, mature eggs from paratype.

cotylophore' which is 2.4–4.2 mm long by 2.8–3.8 mm wide and extends on the ventral side from behind the posterior end of the ovary to a considerable distance back of the posterior end of the body proper. In the type this cotylophore begins in the midventral region at the level of the junction of the middle with the posterior third of the entire body with a smooth semicircular fold 1.2 mm wide which is followed by a twisted, fan-shaped body fold fringed with a semicircular row of 18 or 19 long-stalked clamps. For convenience of reference the clamps are numbered from in front backwards; the first clamp next to the semicircular fold is the smallest (about 0.2 mm in diameter), rather short-stalked, the 12th may be slightly out of the row of other clamps, the 14th to 16th are the largest (up to 0.45 mm in diameter), with longer stalks, and the last 18th (19th in one paratype) attached to the right posterior end of the body proper is provided on the proximal anterior margin of its stalk with a blunt-conical or subcylindrical caudal appendage 0.15–0.16 mm long. This caudal appendage is armed in the type with a small guarded apical hook 35μ long and two dissimilar subapical hooks, one of which is 77μ long and guarded like the apical hook, but the other is simple, falcate and 37μ long lineally. In the paratypes either the guarded subapical or the falcate hook is absent (see Fig. 7C), so that the armature of this appendage is variable. Clamp skeleton 0.18–0.46 mm in diameter, consisting of an arcuate, perforated, median spring, and two pairs of curved lateral arms articulating with each other, of which the smaller pair articulates at the distal end with a small λ -shaped accessory sclerite.

Head end rounded; mouth aperture wide, subterminal; oral suckers paired, muscular, septate, $53\text{--}81 \times 65\text{--}93\mu$; pharynx oval, weakly muscular, $116 \times 98\mu$ in the type. Esophagus simple, 0.5–0.7 mm long, bifurcating a little behind genital pore. It is not certain whether the intestinal limbs are confluent posteriorly or not; there are wide anterolaterally directed diverticles on each side anteriorly (Fig. 7D), the remaining greater part with few short inner, and numerous longer, subdivided, outer branches accompanied by vitellaria and pigment

cells; posterior outer branches extending into basal portion of clamp stalks.

Testes rounded, about 50 in total number, arranged in two zigzag longitudinal rows, one on each side of median line; anterior ones pre-ovarian, posterior ones para-ovarian, some between ovarian limbs. Vas deferens straight or gently undulating in median field, surrounded at its distal end by prostate cells; no pars prostatica differentiated. A distinct globular bulb of very fine muscle fibers is developed around the somewhat swollen distal end of the ejaculatory duct. Cirrus represented by a cylindrical group of very fine acicular spines, enclosed basally in a crown of 18 hooks, which in turn is enclosed in the atrial bulb with thick walls of radial muscle fibers. The hooks are fused near the base, and their simple attenuated points are curved inwards. This thick-walled atrial bulb is $51\text{--}80\mu$ in outside diameter, and enclosed entirely in the genital atrium with a membranous wall. Genital pore midventral, immediately in front of the above mentioned thick-walled atrial bulb, 0.5–0.7 mm from head end.

Ovary inverted U-shaped, 2.35 mm long by 0.4 mm wide as a whole in the type, enlarged at proximal end to an elongate compact mass, situated to right of median line in middle third of body. Genito-intestinal duct arising from germiduct just before the latter unites with the stem of the vitelline reservoir. Ootype postero-sinistral to this genital junction. Uterus proper alongside vas deferens, opening into genital atrium ventral to male duct. Mature eggs elongate oval, $0.25\text{--}0.26 \times 0.11\text{--}0.15$ mm, with a rigid filament at each pole; anterior filament 0.19–0.26 mm long, posterior filament 0.12–0.2 mm long, slightly enlarged at tip. Genito-intestinal duct running straight obliquely forward and emptying into right intestinal limb, with distinct accompanying cells. Vaginae indistinct in the type, but present on each side in form of a ventrosubmarginal longitudinal row of several rudimentary areolae just behind level of symmetrical excretory pores in one of the paratypes. Vitelline reservoir Y-shaped, with short arms. Excretory pores symmetrical, dorsal, submarginal at about level of genital pore or a little posterior to it.

DISCUSSION: This genus is very closely related to *Allospseudaxinoides* Yamaguti, 1965,² in general internal anatomy, but differs from it in the arrangement of clamps and in possessing septate oral suckers but no reticular anastomosis of the anteriormost vitelline ducts. On the basis of these differences I prefer to create the new genus *Cypselurobranchitrema*, for which a new subfamily Cypselurobranchitrematinae is suggested, because this genus cannot be assigned to Allospseudaxininae Yamaguti, 1963.

Cypselurobranchitrematinae n. subfam.

SUBFAMILY DIAGNOSIS: Axinidae. Body elongate, moderately wide. Opisthaptor twisted fan-shaped, attached on ventral side of body proper at its posterior end, fringed with a number of stalked clamps in semicircular row. Oral suckers paired, septate, within oral cavity. Intestine strongly ramified. Testes numerous, pre- and paraovarian. Genital atrium enclosing armature of complex structure, opening mid-ventrally. Ovary tubular, in midregion of body. Genito-intestinal duct present. Eggs filamented. Paired vaginae rudimentary or absent. Vitellaria coextensive with intestine and its branches. Gill parasites of marine fishes.

Cypselurobranchitrema n. g.

GENERIC DIAGNOSIS: Axinidae, Cypselurobranchitrematinae. Body moderately large, abruptly tapered anteriorly. Opisthaptor asymmetrical, arising from posterior midventral region of body proper, with a twisted semicircular body fold, which is followed by a fan-shaped fold fringed with a semicircular row of a number of stalked clamps; clamp skeleton similar to that of *Allospseudaxinoides* Yamaguti, 1965. Caudal appendage with anchors of different shape and size on stalk of last clamp. Intestinal limbs with short inner and longer outer branches. Testes small, arranged in two longitudinal rows, pre- and para-

ovarian. Prostate cells around distal end of vas deferens; ejaculatory duct enclosed in muscle bulb. Cirrus represented by a cylinder of very fine acicular spines, surrounded basally by a ring of hooks, which in turn is enclosed in atrial bulb with thick walls of radial muscle fibers. Genital atrium opening ventral to esophagus. Ovary inverted U-shaped, submedian, in midregion of body. Genito-intestinal duct opening into right intestinal limb. Eggs with rigid filament at each pole. Vitelline follicles small, largely coextensive with intestine and its branches, with which they extend into the stalk of clamps. Vaginae indistinct or opening symmetrically on ventral submarginal surface a little behind level of genital pore. Parasitic on gills of marine teleosts.

TYPE SPECIES: *C. spilonopteris* n. sp., on *Cypselurus spilonopterus*; Hawaii.

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² The original diagnosis of this genus is emended as follows: "Vaginae rudimentary, opening dorso-submarginally at about level of genital pore or absent. Anteriormost vitelline ducts of two sides with reticular anastomosis."

North American Harpacticoid Copepods, 8
The *Danielssenia sibirica* Group, with Description of
D. stefanssoni Willey from Alaska

MILDRED STRATTON WILSON¹

WILLEY'S REPORT (1920) on marine copepods of northern and northwestern coastal waters of North America included 12 species of Harpacticoida, mostly from Canadian inshore localities. Among these was a new species, *Danielssenia stefanssoni*, of particular interest because of its relationship to *D. sibirica* Sars from the northeastern Siberian coast. Lang (1944, 1948) divided the six species of the genus into two groups. One, called the *sibirica* group, includes only these two related species occurring in closely situated regions of neighboring continents. The present paper extends the known distribution of *stefanssoni* to the Chukchi Sea coast of Alaska, placing it not far distant from the nearest Asian occurrence of *sibirica* on Wrangell Island. Considering the scant knowledge of harpacticoid copepods of these two continental regions, it is not certain that the geographic separation is real, although it may be since such allopatry is suggested by other species-pairs and groups of freshwater, brackish-water, and marine copepods.

The possible existence of a species-pair on the two continents is of considerable zoogeographic interest and phylogenetic importance. Accurate determinations of the two species and of possible unknown species, recognition of variations, and phylogeny of the group and genus require detailed anatomical knowledge of *D. stefanssoni*. For these reasons, I have prepared this account of Alaskan specimens. A synopsis of literature, distribution, and comments on anatomy of *D. sibirica*, necessary for critical comparison with *stefanssoni*, are included.

¹ Arctic Health Research Center, U. S. Public Health Service, Anchorage, Alaska and Smithsonian Institution. Manuscript received August 9, 1965.

Family TACHIDIIDAE

Genus *Danielssenia* Boeck, 1872

typica group (emendation of Lang, 1948):

D. typica Boeck, *D. fusiformis* (Brady)
sibirica group (after Lang, 1948):

D. sibirica Sars, *D. stefanssoni* Willey
unassigned species (emendation of Lang, 1948):

D. robusta Sars, *D. perezi* Monard

COMMENTS ON LITERATURE: Lang assigned four of the six species of the genus to the *typica* group, of which only *D. typica* and *D. fusiformis* are known from both sexes. Since the modification of leg 2 of the male is an important character defining the two groups, the other two species (*robusta*, *perezi*) cannot be placed in any group at present, their relationship to all other species and to one another being considered indefinite. Even though they conform to the *typica* group in the number of setae on certain segments of the antennal exopod and of leg 4, they differ strikingly in forms of female leg 5 and in comparative lengths of endopod to exopod of legs 2-4. Although it may at times be true, it should not be considered incontrovertible that the number of setae of any given appendage is always a measure of degree of relationship of species in the Harpacticoida. An example of an undoubted species-pair that seemingly occurs allopatrically on the Eurasian and North American continents is that of *Bryocamptus cuspidatus* and *B. tikchikensis*. The latter, described from Alaska (Wilson, 1958) and since found in Greenland (Røen, 1962), differs principally from the Eurasian *cuspidatus* in having 1 instead of 2 inner setae on exopod segment 3 of leg 3.

The form of female leg 5 of the *D. sibirica*

group is very like that of the two species of the *typica* group and may indicate a closer relationship to that group than is true for *robusta* and *perezi* with their strikingly different structure of this appendage. In classification of all Copepoda, it seems to me that form of appendages must be considered along with numerical aspects, such as numbers of segments and setae.

Lang (1948) incorrectly ascribed authorship of *D. fusiformis* to Brady and Robertson, 1876, a nomen nudum. The species, listed by these authors as *Jonesiella fusiformis*, n. gen., n. sp., dates from the description by Brady (1880). Sars (1909:336) mentions a species *D. brucei*, supposedly described by T. Scott. So far as I have been able to ascertain, this is an erroneous reference to *Cyclops brucei* T. Scott.

THE *sibirica* GROUP

sibirica group: Lang, 1944, p. 9 (original definition); 1948, p. 298 (emended def.; inclusion *D. stefanssoni*).

Lang interprets the stout spinous projection of the inner margin of segment 1 of the endopod of male leg 2 as a transformed seta. Whether this process is a modified seta or an enlarged projection of the segment itself can be determined only by study of developmental copepodid stages. Until such information is available, it seems best to me to emend the definition of the group by referring to this as a process or a "projection" of the segment, as Sars (1898) has done.

Danielssenia sibirica Sars

Danielssenia sibirica Sars, 1898, p. 343, pl. 10, figs. 1–20.

Danielssenia sibirica: Yashnov, 1935, pp. 127, 134, fig. 6 (occurrence; notes on length; fig. leg 5 ♀).—Lang, 1948, p. 282, table 5 (leg setation); p. 298 (taxonomic group; key); p. 301, fig. 146.5 (figs., diagnosis from Sars).—Borutzky, 1952, p. 105, figs. 37, 38 (description, figs. from Sars).

COMMENTS ON LITERATURE: Sars has undoubtedly confused female legs 3 and 4. In the text, he states they have the same number

of setae (3) on the inner margin of the endopod, differing from the male with only 2 setae. His Figure 12 is labeled leg 4, but since the length of its endopod is similar to that of *D. stefanssoni* shown here (Fig. 2C), it seems logical that Sars's Figure 12 was drawn from leg 3, leg 4 being illustrated only for the male of *sibirica*. Lang (1948: Table 5; p. 298) has rightfully questioned this setation. Sars also found no setae on female exopod segment 1 of legs 2 and 3 (his leg 4), but illustrated them in male legs 3–4. The copy of Sars's paper used in my study is a reprint autographed by Sars as a presentation copy to G. S. Brady and now part of the library of the Division of Crustacea, U. S. National Museum. All of the figures of the legs, in which this seta is not clearly shown, have indistinct lines where the seta should be, if present, suggesting partial erasure or inadequate reproduction. Sars (p. 325) expressed dissatisfaction with the reproduction of his drawings, commenting that "the finer shadows in the figures have been to some extent lost." It is possible, therefore, that an inner seta is present in both sexes of *sibirica* on exopod segment 1 of legs 2–4, as in *stefanssoni*. (See also comments in description of *D. stefanssoni* below.)

An aesthete occurs on segment 4 of the female antennules of both *sibirica* and *stefanssoni*, and the 5-segmented antennule of *sibirica*, if correctly depicted, results from fusion of two segments of the apical part. This is clearly separated into two segments in my specimens of *D. stefanssoni*, resulting in the 6-segmented antennule also noted by Willey (see Fig. 1G herein). Other differences that may be real or not exist in the numbers of setae of parts of the other cephalic appendages, such as the apex of the antennal endopod. Sars, like Willey, has shown the seta of the end claw of the maxilliped arising near the apex, a probable error by both authors (see Fig. 1E herein).

It seems to me, in comparing Alaskan specimens of *D. stefanssoni* and the original descriptions of the two species, that they differ very little and may actually be separable by fewer differences than is apparent in the literature. The most reliable distinction seems to be that found in the reduced third segment of the

endopod of male leg 2 (the extended apical process of *D. stefanssoni*, absent not only in *sibirica* but also in other species of the genus).

DISTRIBUTION AND ECOLOGY: Type locality not designated. Sars records collections made in August–September, 1885–1886, from three localities of the coastal regions of Siberia and islands between the Laptev and East Siberian seas, including the lower part of the River Yana and the New Siberian Islands. Of these, only one collection was taken from the sea, the others having been made in what must have been brackish situations. Yashnov's record from Wrangell Island, overlooked by Lang (1948), was based on 1929 collections from brackish water. The range of distribution of *D. sibirica* as now known is therefore from about 72°–74° N and 135°–180° E, and it should be classified as a brackish water-marine species.

Danielssenia stefanssoni Willey, new description
Figs. 1–3

Danielssenia stefanssoni Willey, 1920, pp. 3*k* (reference to), 5*k*, 8*k*, 35*k* (occurrences); p. 39*k*, figs. 60–67 (original description).

Danielssenia stefanssoni: Jespersen, 1939*a*, pp. 78, 100: Table 7 (occurrence; identified K. Lang); 1939*b*, pp. 47, 57: Table 1; p. 58 (occurrence).—Lang, 1948, p. 282: Table 5 (leg setation); p. 298 (taxonomic group; key); p. 301, fig. 146.6 (figs., diagnosis from Willey); p. 1570 (zoogeography).

Danielssenia stepanssoni (incorrect spelling): Mohr et al., 1961, p. 221 (occurrence; identified M. S. Wilson).

Danielssenia: Wilson and Tash, 1966, p. 574 (occurrence).

All of Willey's material was from the region of Bernard Harbour, Canada. No type material is deposited in the National Museum of Canada or the U. S. National Museum (personal correspondence, Dr. E. L. Bousfield and Dr. T. E. Bowman). Willey's description gives only a few figures and notes, some incomplete or differing from Alaskan specimens; many of the notes are written as comparisons with Sars's

nearly complete textual and illustrative account of *D. sibirica*, or of other species. Lang's brief diagnosis appears to be based on Willey's account without addition of any new information from the east Greenland specimens he identified for Jespersen. The few differences between Willey's account and mine are, I believe, logically regarded as errors or omissions rather than variations from the specimens of the type locality. Comments on these and Lang's interpretation, where different, are inserted in parentheses in the following descriptive text. Willey's eight figures illustrate these appendages: antenna (apical segment endopod δ); maxilliped; leg 3 φ endopod; leg 5 φ (2 figs., normal and aberrant); leg 2 δ (2 figs. endopod, entire and enlarged segment 3); leg 3 δ endopod.

OCCURRENCE OF ALASKAN SPECIMENS: NUWUK LAKE (OR POND), Point Barrow Peninsula (71°23'N, 156°28'W); collectors, R. Lewis and J. Tibbs; in three samples taken during ice-free period, 1960: (1) bottom sample, station at 0.9–1.2 m depth, August 1: 12 φ , 1 δ ; (2) horizontal plankton tow south to north, from 0.3 m to surface, August 11: 1 ovigerous φ ; (3) plankton tow, center of lake, from 3.7 m to surface, August 11: 3 φ , 1 δ .—COAST OF CHUKCHI SEA, south of Cape Thompson; plankton samples from two ice-free, landlocked, shallow lagoons (depth not more than 3 m); June 21, 1960; collector, J. Tash: (1) Mapsorak Lagoon (68°02'N, 165°21'W): 3 δ ; (2) Pusigrak Lagoon (68°01'N, 165°18'W): 1 δ .

DESCRIPTION OF FEMALE: Habitus (Fig. 1*A*)—Length range Nuwuk Lake specimens, dorsal midline, base of rostrum to end of caudal rami, 1.25–1.4 mm. Anterior part of body a little shorter and broader than posterior. Distal margins of metasome segments armed with fine spinules. First urosome segment (somite of leg 5) with small lateral processes armed with spinules (Figs. 1*A*, 2*E*). Genital segment divided by cuticular sclerotization ventrally (Fig. 1*C*) and in part dorsally (Fig. 1*A*); ornamented by a few spinules dorsally but not ventrally. External genital area as in Figure 1*C*; genital pore prominent, set at top of

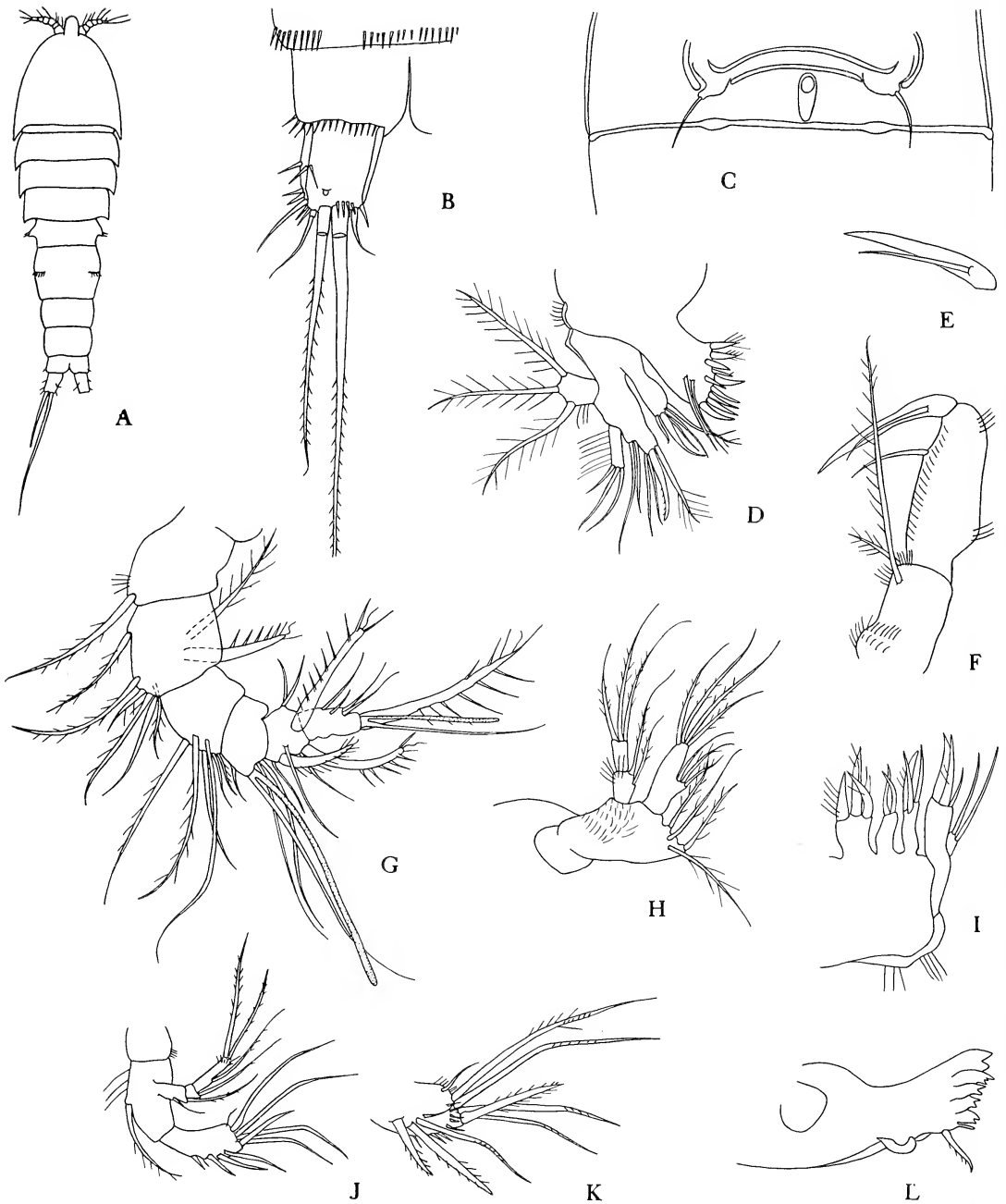


FIG. 1, A-L. *Danielssenia stefanssoni*, Female: A, Habitus, dorsal; B, detail distal segments urosome and caudal rami, ventral; C, external genital area and leg 6; D, maxillule; E-F, maxilliped (E, apical claw with seta, F, entire); G, antennule; H, mandible palp; I, maxilla; J-K, antenna (J, entire, K, detail apex); L, mandible, gnathal blade with outline of insertion point of palp. (B-C drawn to same scale; D-I, K-L enlarged to same scale as one another; J same scale as legs 1-5 shown in Fig. 2.)

elongate-oval structure centralized above cross-wise sclerotization; leg 6 a single seta arising from prominent lobe at each side of genital field. Other urosome segments ventrally with distal rows of spinules consisting of lateral groups of stout spinules and a more slender medial group irregular in length, as partially shown in Figure 1B; anal segment deeply cleft in middle; row of spinules overlying bases of caudal rami. Caudal ramus (Fig. 1B) a little longer than outer margin of anal segment (about 1:0.76) and its own greatest width at base (about 1:0.88); with lateral and apical groups of spinules; dorsal seta near middle; other caudal setae placed apically or subapically: the two outer marginal setae of similar length to one another and to ramus, the proximal subapical, the distal seta apical; two stout apical spinulose setae, jointed near bases, the middle about twice length of outer seta and less than that of urosome; innermost apical seta little shorter than lateral setae. Rostrum (Fig. 1A) nearly twice as long as wide, nearly equaling length of proximal three segments of antennule; apex truncate; base not demarcated from cephalosome. (Habitus characters agree with the few given by Willey, except that he describes the rostrum as "defined behind.")

Antennule (Fig. 1G). First 4 segments of similar width, proximal 3 subequal in length to one another, the fourth reduced to half their length; last 2 segments reduced in width, the sixth narrower and longer than fifth (Willey gives their length as identical). Aesthetes of segments 4 and 6 arise on common base with a slender seta. Number of setae and aesthetes:

Segment	1	2	3	4	5	6
Setae	1	8	6	4	8	6
Aesthetes				1		1

Segments 2 and 6 bear 1 seta, and segment 5 bears 3 stout, modified setae, armed with large spinules and tipped with hairlike setules. Other setae are plumose or naked as shown in figure.

Antenna (Figs. 1J–K). Allobasis with 1 long marginal seta reaching to about middle of apical segment (endopod). Exopod segment 1 with 2, segment 2 with 1 and segment 3 with 1 lateral and 2 apical setae (presence of 2 setae on segment 1 distinguishes *sibirica* group in part

from other species of the genus). Distal endopod segment (Fig. 1K) with marginal group of 2 stout spines and longer modified seta similar to apical "geniculate" setae (this seta is the one referred to by Willey as "long curved claw"); apically, 6 elements consisting of 1 stout spine, 3 modified "geniculate" setae, a longer sparsely plumose seta, and a short, slender seta placed subapically (this latter seta omitted by Willey).

Mandible. Gnathal blade (Fig. 1L) with 5 bifurcate denticles, a single denticle, and a stout subapical spiniform seta. *Palp* (Fig. 1H): Basis with 4 setae; endopod unsegmented with 3 lateral and 4 apical setae; exopod 2-segmented, bearing 2 and 3 setae respectively.

Maxillule (Fig. 1D; "maxilla" of Willey of which only exopod setae were mentioned in text). Gnathal lobe prominently produced, bearing 2 surface setae and 10 stout apical spines. Coxa and basis not separated, bearing 2 elongated laciniae, the first with 5 apical setae, the second (representing the basis) with 2 lateral and 4 apical setae, one a stout spine. Endopod and exopod unsegmented, each with 3 setae; those of exopod the longest of entire appendage.

Maxilla (Fig. 1I; not described by Willey). With 4 stout, well-defined endites; number of setae and modified spines from proximal to distal endite: 3, 2, 3, 3. Endopod distinct with 2 long slender setae.

Maxilliped (Figs. 1E–F). Essentially as figured by Willey, except that accessory seta of claw arises near base rather than near apex (Fig. 1E). (Willey's figure, copied by Lang (1948), shows only the apex of the seta which makes it appear very short and as arising beyond the middle of the claw, as Sars (1898) has also, probably incorrectly, shown it for *D. sibirica*.)

Legs 1–4 (Figs. 2A–D). Endopod of leg 1 reaching to end of or little beyond exopod; that of leg 2 reaching end of exopod, progressively shorter in legs 3 and 4, so that in leg 4 it reaches to only a little beyond exopod segment 2. Outer distal edge of endopod segments 1 and 2 produced in legs 2–4, most pronounced in segment 2 of leg 3 (as noted and figured by Willey). Apical setae of exopods and endopods of legs 2–4 somewhat spiniform, inner setae

very slender. Setation of legs summarized in Table 1. (Willey has illustrated only the endopod of leg 3, and given only the setation of segment 3 of both rami in the text. These agree with my Alaskan specimens. Lang (1948:282) has included setation for segments 1 and 2 of the female exopods and endopods in his Table V, although such information is available from Willey's account for only the endopod of leg 3. As shown here in Table 1 and in Figure 2, the first segment of the exopods of both sexes bears a seta, unlike the other species of the genus, although *D. robusta* may have a rudimentary seta on exopod 1 in leg 4, if the figure given by Sars (1920:Pl. 64) is correct. See also comments above under *D. sibirica*.)

Leg 5 (Fig. 2E). Exopod broader than long, with 5 setae, depressed gap between setae 4 and 5. Basal expansion elongate, reaching beyond exopod (longer than in Willey's Figure 63); with 5 setae arranged as in figure.

DESCRIPTION OF MALE: Length range—NUWUK LAKE, 0.94–1.0 mm; CHUKCHI SEA COAST lagoons, 1.0–1.2 mm. Habitus as in female except that segment bearing leg 5 lacks lateral processes, and genital segment is completely divided.

Antennule (Fig. 3). 5-segmented plus a reduced apical part divided into 3 or 4 portions, the last clawlike and armed with tuft of 3 or more hairlike setae; segments 1–2 usually incompletely separated. (Willey states that the antennule is as figured by Sars (1909) for *D. typica*, shown as having the same number of segments as in my specimens.) Segment 3 subequal to length of 1 + 2, with 10 well-devel-

oped setae, half of which are plumose; 2 setae near outer margin spinelike, set on raised papillae, armed with spiculate setules. Segment 4 presumably with considerable flexibility of outer margin permitting contraction or expansion that controls, at least in part, movement of expanded apical area and its claw; the partial line drawn inwards from the margin in Figure 3 is not an incomplete segment but a surface line resulting from contraction; in less expanded appendages, several of these lines may be seen. Segment 5 greatly enlarged and ornamented (since Figure 3 has been drawn from dissections studied at high magnifications with both dry and oil immersion objectives, it probably shows details common in the genus but not previously illustrated in literature); inner margin broken into 3 processes, the first dentate, the second ridged, the last two produced at their distal ends; surface adjacent to these processes a hollowed area from which arise 4 short, plumose setae; this area defined by stout, sclerotized ridge beginning near proximal part of segment, running nearly its entire length and ending in stout papilla from which an aesthete and 2 setae arise, aesthete jointed near distal third; 3 slender, closely set setae at base of ridge and a similar seta near apex. Number of setae and aesthetes:

Segment	1	2	3	4	5
Setae	1	1	10	4	10
Asthetes					1

Other cephalic appendages like those of female.

Legs 1–4 (Figs., 2A, G–L). Inner spine of basal segment 2 of leg 1 more slender than that of female (Fig. 2A). Form and setation of

TABLE 1
SUMMARY OF SETATION LEGS 1–4 OF *Danielssenia stefanssoni* ♀ ♂ *

SEGMENT	EXOPOD			TOTAL SEG. 3	ENDPOD			TOTAL APICAL SEG.
	1	2	3		1	2	3	
Leg 1 ♀ ♂	sp-O	sp-s	3sp-2s-O	5	O-s	O-sp,2s-s		4
Leg 2 ♀	sp-s	sp-s	3sp-2s-2s	7	O-s	O-s	sp-2s-2s	5
Leg 2 ♂	sp-s	sp-s	3sp-2s-2s	7	O-pr	pr-O	O-pr-4s	4
Leg 3 ♀ ♂	sp-s	sp-s	3sp-2s-3s	8	O-s	O-s	sp-2s-3s	6
Leg 4 ♀ ♂	sp-s	sp-s	3sp-2s-3s	8	O-s	O-s	sp-2s-2s	5

* Explanation of symbols: Seg. = segment; sp = spine; s = seta, including long, spiniform setae; pr = process. Arrangement of armature for each segment from outer to inner margin. Position on apical segment shown by the symbol "'-" indicating outer, apical, and inner margins respectively; or by "'," dividing distinct spines and setae of apex.

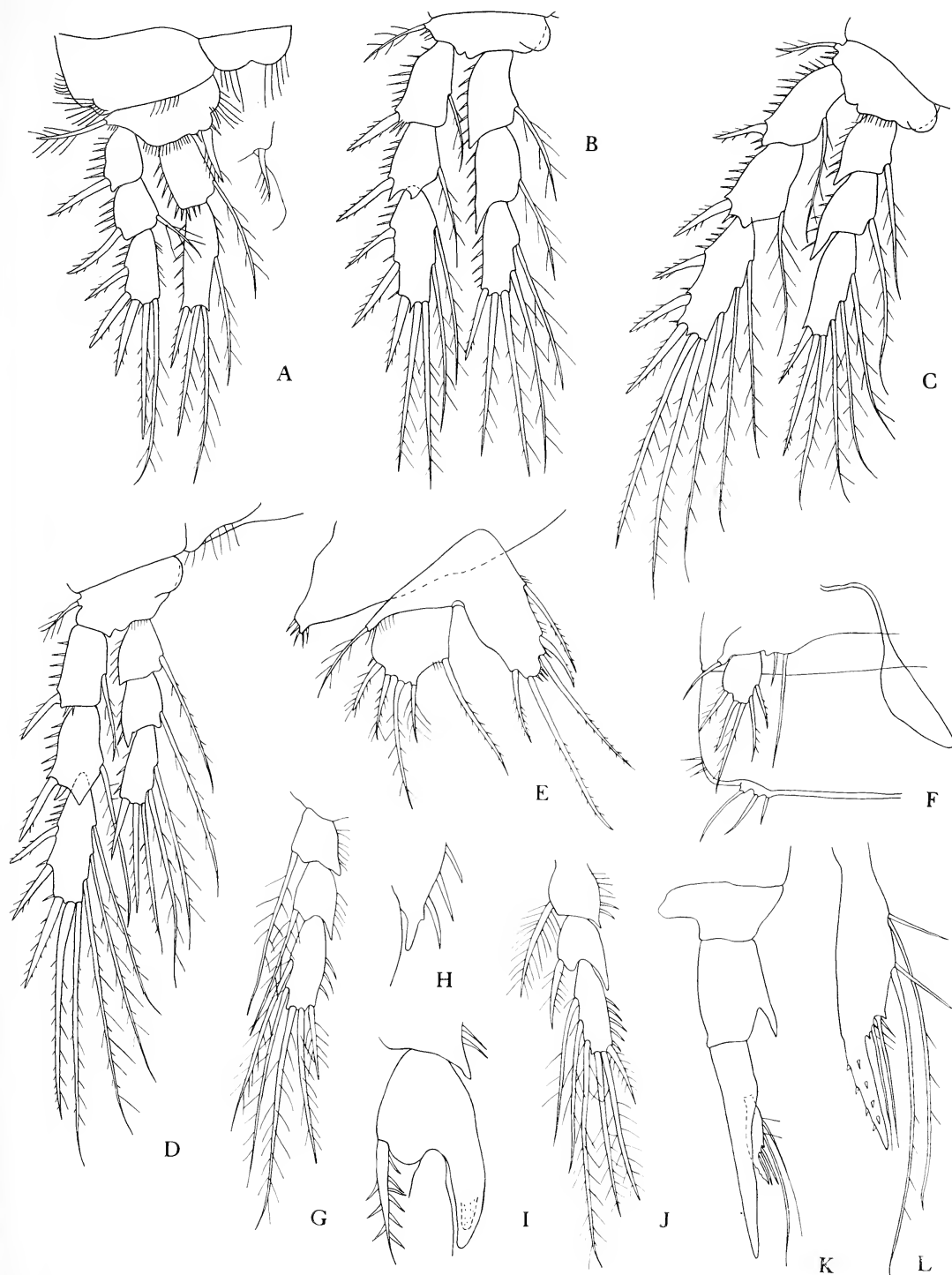


FIG. 2, A-L. *Danielssenia stefanssoni*. A-E, Female: A, Leg 1 and detail inner spine basal segment 2 of male; B, leg 2; C, leg 3; D, leg 4; E, leg 5 and produced edge of body segment. F-L, Male: F, Legs 5-6, in situ, with outline of spermatophore in body; G-H, endopod leg 4 (G, entire, H, enlarged distal outer margin segment 2); I-J, endopod leg 3 (I, enlarged segment 2, J, entire); K-L, endopod leg 2 (K, entire, L, enlarged segment 3). (All drawn to same scale as one another except those indicated as enlarged.)

exopods as in female (Figs. 2A–D; Table 1). Endopods of legs 2–4 more or less modified, all except that of leg 2 similar in length and setation to female (Table 1). That of leg 2 (Figs. 2K–L) of general form found in genus; segment 1 with inner spurlike process and lacking seta; outer margin of segment 2 produced distally as long process reaching beyond apex of exopod by nearly half the length of entire segment. Segment 3 reduced, about one-third length of segment 2, inserted deeply into inner part of proximal third of segment 2; inner apex produced as stout process nearly one-third total length of its segment, armed with raised surface spinules; inner margin with 4 slender setae, the proximal two reaching beyond apex of segmental process, each set sparsely with fine hairs and having a long spinule at its base; the distal two set closely together in recess at base of segmental process, reaching to its apex or a little beyond (Fig. 2L). (Willey has shown only 1 distal seta in his figure, which is undoubtedly incorrect since the setae are closely set and difficult to distinguish from one another, and illustrations of other species of the genus show 2 distal setae.) Modification of leg 3 largely affecting segment 2 (Figs. 2I–J), which is enlarged both inwardly and outwardly; apex of outer enlargement produced distally, blunt, of thickened cuticle into which inner tissue does

not penetrate (Fig. 2I) (neither stained nor unstained material studied in different views at various magnifications with both dry and oil immersion objectives showed any incision such as illustrated by Willey; where this exists it is probably an insignificant, individual variation); inner part of segment enlarged, with distal lobe and stout, short seta (Fig. 2I); segment 3 constricted basally, bearing 6 spines and setae as in female. Leg 4 endopod (Figs. 2G–H) very similar to that of female; segments 1 and 2 with slightly more acuminate margins.

Leg 5 (Fig. 2F). With 5 setae on exopod, variable in length from one specimen to another but seta 3 (from outer margin) always the longest; basal part hardly produced, with 2 (or sometimes 3) setae, seta 2 the longer. Leg 6 with 3 setae, the outer the longest.

DISTRIBUTION AND ECOLOGY: The type locality was not designated and must be considered to be generalized in the Bernard Harbour region of Dolphin and Union Strait. Bernard Harbour (about 69°09'N, 114°40'W) is on the mainland of Canada near the eastern end of the strait which separates the mainland from Victoria Island, one of the island group marking the eastern limits of the Beaufort Sea. The number of specimens and sex are listed for some of Willey's records, but none include both sexes. The specimens occurred in plankton tows, mostly surface, with copepods of the three major free-living orders. References to depth of water at stations are not always given or are indefinite; greatest depth of water recorded is 3 fms (5.5 m). Salinity is not given. Collections were presumably made in ice-free water between August 9 and September 30, 1915.

Greenland records are from the eastern coast of the Denmark Strait separating Greenland from Iceland. Collections were made July 14–September 8, 1932, at Barclay Bugt, 69°15'N, 24°50'W (Jespersen, 1939a), and at Kangerdlugssuaq, about 68°18'N, 32°20'W (Jespersen, 1939b). The reference of Mohr et al. (1961) is to Nuwuk Lake, Point Barrow, Alaska, and that of Wilson and Tash (1966) to the Cape Thompson region of the Alaskan Chukchi Sea coast, for both of which detailed records are given above under the section, "Occurrence of Alaskan Specimens." All



FIG. 3. *Danielssenia stefanssoni*, Male: Antennule (same scale as Fig. 1G).

known records are north of the Arctic Circle. The range of distribution is from the east central coast of Greenland to the Chukchi Sea coast of Alaska, from about 68°–71° N and 24°–165° W.

All collections of Willey and Jespersen were from coastal plankton tows. Those of Willey were probably made in brackish waters. The Alaskan records are from landlocked coastal bodies of water. Nuwuk Lake has been described by Mohr et al. (1961) and Holmquist (1963), and features relative to its copepod fauna are given in Wilson (1965). Significant features are: surface area about 2.5 ha; maximum depth 5.2–5.6 m; slightly brackish surface waters (about 5–8 o/oo); bottom salinity about 60 o/oo; ice-free period 2 months or less (July–August). Copepod associates of *D. stefanssoni* were species of marine and brackish waters having varying degrees of euryhalinity within genus or species.

Lagoons of the Cape Thompson region have been studied with respect to their copepod fauna by Johnson (1961) and Wilson and Tash (1966). Collections were made only as plankton tows and harpacticoids were rare in the samples examined by me from eight lagoons, reflecting the method of sampling rather than the actual presence or absence of the group. Although *D. stefanssoni* was found in only two lagoons, it may well be a habitant of most of the lagoons along the coast.

Physical features of the lagoons are relatively low salinity, shallow depth (maximum, 3 m), and freedom from ice cover for about 2½–3 months. Salinity recorded on several dates in 1959–1961 for Pusigrak Lagoon was always very low (0.08–0.35 o/oo). Mapsorak Lagoon likewise had very low salinity (0.4–0.87 o/oo) in 1960–1961 when *D. stefanssoni* was collected, but Johnson recorded salinity of 14.31–15.96 o/oo in August 1959, at which time a large number of neritic calanoid species were present. Since these were not collected in 1960–1961, it has been assumed that the lagoon had been flooded with sea water during a storm and at least part of the copepod community was temporal (Wilson and Tash, 1966).

In the literature and new records given herein, collections have all been made by plankton tows, and *D. stefanssoni* occurred only

in small numbers, mostly as adults in middle-late summer. Presence of adults in late June in Cape Thompson lagoons, as contrasted with later dates in the Barrow region, may be due to earlier development resulting from higher temperatures earlier in the season with a longer period of ice-free water. Most records seem to indicate that maturity of the summer generation is attained late in the season and that the adults have some degree of planktonic motility. Knowledge of the life history of the species, through occurrence of its developmental stages, apparently can be acquired only by methods directed specifically at collection of harpacticoids during what represents early summer for any given region.

ACKNOWLEDGMENTS

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Notes on Occurrence of Young and Spawning of *Scomberomorus sierra* in the Eastern Pacific Ocean

W. L. KLAWE¹

ABSTRACT: Young of *Scomberomorus sierra* are briefly described and compared with young of other scombroids and some other related families. At sizes of 30–50 mm of total length young *S. sierra* can be distinguished from *S. concolor* on the basis of gill raker counts.

From this study, based on the collection of larvae and juveniles of *S. sierra*, it is evident that this species spawns near the coast over most of its distributional limits. Spawning off Mexico takes place in July through September and in lower latitudes from perhaps December through April.

RESUMEN: Los juveniles de *Scomberomorus sierra* se describen brevemente y se comparan con los juveniles de otros escombroides y con algunas otras familias afines. Cuando alcanzan la longitud total de 30 a 50 mm los juveniles de *S. sierra* pueden ser distinguidos de los de *S. concolor* en base al recuento de las branquiaspinas.

Es evidente, según este estudio basado en la recolección de larvas y juveniles de *S. sierra*, que estas especies desovan cerca a la costa en la mayor parte de sus límites de distribución. El desove frente a México toma lugar de julio a septiembre, y en las latitudes más bajas probablemente de diciembre a abril.

THE GENUS *Scomberomorus* is represented in the eastern Pacific Ocean by two species, *S. sierra* and *S. concolor*, the sierra and the Monterey Spanish mackerel, respectively. The Spanish name most commonly applied to both species is "sierra." The distribution of *S. sierra* extends from California south to Peru and around the Galapagos Islands (Hildebrand, 1948; Roedel, 1953; Berdegúe, 1956; and Collette et al., 1963). *S. concolor* ranges from California to perhaps as far south as the Gulf of Panama; in the last century it was fished commercially in the waters off California, but at present is considered to be rare there. The center of distribution of *S. concolor* appears to be the Gulf of California (Fitch and Flechsing, 1949). The uncertainty concerning the distribution of *S. concolor* is due to its superficial resemblance to *S. sierra*. The number of gill rakers on the first gill arch is the main character which distinguishes the two species from each other; counts for adults of the two species are:

SPECIES	UPPER ARCH	LOWER ARCH
<i>S. sierra</i>	2–4	10–12
<i>S. concolor</i>	5–9	15–20

Little is known of the spawning and early life history of the two species, especially of *S. concolor*; the only published information pertains or appears to pertain to *S. sierra*. According to Walford (1937), "sierra" in Mexican waters spawn probably in late spring or summer. Eckles (1949) indicates that in the more southern waters, particularly off Costa Rica, the time of spawning is most likely January and February. Clemens (1956) substantiated Eckles' conclusion by collecting juveniles of *S. sierra* in the Gulf of Panama in early February. The closely related Atlantic species, *S. maculatus*, spawns over a period of 6–10 weeks. The time of spawning is later in the northern parts of the Atlantic coast of the United States than in the southern parts (Earll, 1882).

While collecting young stages of tunas by means of dip-netting under a night light from commercial fishing vessels and research ships in waters of the eastern Pacific Ocean, staff mem-

¹ Inter-American Tropical Tuna Commission, La Jolla, California. Manuscript received June 9, 1965.

TABLE 1
RECORDS OF CAPTURE OF LARVAL AND JUVENILE *Scomberomorus sierra* FROM THE EASTERN PACIFIC REGION

DATE	GENERAL LOCALITY	LATITUDE	LONGITUDE	SIZE IN MM ¹	NO.	REFERENCE OR COLLECTOR
Jan. 29, 1912	Naos I., Gulf of Panama			107	1	Meek and Hildebrand (1923) ²
July 26, 1913	Chame Pt., Gulf of Panama			12-67	20	Meek and Hildebrand (1923) ²
Feb. 11, 1937	Ft. Amador, Gulf of Panama			92	1	Komp ²
Feb. 26, 1937	Venado Beach, Gulf of Panama			59	1	Komp ²
March 24, 1939	Potrero Grande Bay, Costa Rica			26.5-71	8	Eckles (1949)
April 16, 1941	Chilca Bay, Peru			109-139	7	Hildebrand (1946) ²
Sept. 17, 1946	Acapulco, Guerrero, Mexico			"postlarvae and several juveniles"		Hubbs ³
Feb. 1947	Gulf of Nicoya, Costa Rica			50.5	1	Eckles (1949)
Sept. 24 and 25, 1948	Ballenas Bay, Baja Calif., Mexico			21-23.25	3	Eckles (1949)
Aug. 28, 1951	Turtle Bay, Baja Calif., Mexico	27°39.7'N	114°52.3'W	16	1	J. Radovich ⁴
Sept. 13, 1952	Off Boca de Sto. Domingo, Baja Calif., Mexico	25°34'N	112°19'W	4.5 and 9.5	2	? ⁵
March 8, 1953	Cocos Pt., Isla del Rey, Gulf of Panama			30	2	L. R. Rivas ⁶
March 27, 1954	Gulf of Papagayo, Costa Rica	10°31'N	86°12'W	11.5	1	Clemens ⁴
April 18, 1954	Off Nicaragua	11°48'N	87°09'W	23	1	Clemens ⁴
April 19, 1954	Off Nicaragua	11°42.5'N	87°09'W	17	1	Clemens ⁴
Jan. 27, 1955	Charco Azul Bay, Gulf of Panama	8°15'N	82°47'W	13-67	16	Clemens ⁴
Feb. 4, 1955	Gulf of Panama	8°31'N	78°56'W	13-24	12	Clemens ⁴
Feb. 5, 1955	Gulf of Panama	8°06'N	79°06'W	12-58	14	Clemens (1956) ⁴

Jan. 10, 1956	Gulf of Panama			36	1	A. Landa ^{7, 8}
Jan. 14, 1956	Off Punta Foca, Peru			9.5-22	97	G. W. Bane and G. C. Broadhead ⁷
July 9, 1956	Uncle Sam Bank, Off Baja Calif., Mexico	25°34.5'N	113°45.5'W	8.4	1	? ⁵
July 10, 1956	Ballenas Bay, Baja Calif., Mexico	26°39'N	113°11'W	53.5-72.5	8	J. J. Seapin ⁴
July 27, 1956	Sta. Maria Bay, Baja Calif., Mexico	24°45.5'N	112°14.6'W	24-35	5	T. Jow ⁴
July 28, 1956	Magdalena Bay, Baja Calif., Mexico	24°39'N	112°08'W	26-38.5	5	T. Jow ⁴
July 31, 1956	Magdalena Bay, Baja Calif., Mexico	24°32.8'N	112°03.7'W	40	1	C. H. Turner ⁴
Aug. 1, 1956	Sta. Maria Bay, Baja Calif., Mexico	24°42.7'N	112°10.7'W	28-33	15	C. H. Turner ⁴
Aug. 1, 1956	Off Sta. Maria Bay, Baja Calif., Mexico	24°46.1'N	112°15'W	36-42	18	C. H. Turner ⁴
Aug. 12, 1956	Off Boca de Sto. Domingo, Baja Calif., Mexico	25°34.2'N	112°18.7'W	4.8	1	? ⁵
Sept. 23, 1956	Petatlan Bay, Guerrero, Mexico			36	1	Klawe ⁷
April 7, 1957	Acajutla, El Salvador			29	1	Klawe ⁷
Dec. 28, 1957	Farfan Beach, Gulf of Panama			39 + 106	2	P. W. Johnson ⁷

¹ Direct distance from tip of snout to tip of the shortest median caudal ray.² In the collection of the U. S. National Museum, Washington, D.C.³ Fieldbook data of C. L. Hubbs, Scripps Institution of Oceanography, La Jolla, California.⁴ In the collection of the California State Fisheries Laboratory, San Pedro, California.⁵ In the collection of the South Pacific Fishery Investigation of the U. S. Fish and Wildlife Service, La Jolla, California.⁶ In the collection of the University of Miami, Florida.⁷ In the collection of the Inter-American Tropical Tuna Commission, La Jolla, California.⁸ From a stomach of *Euthynnus lineatus*.

bers of the California State Fisheries Laboratory and the Inter-American Tropical Tuna Commission have captured a variety of fish, including juveniles of *Scomberomorus*. As will be shown later, there is reason to believe that most likely all of these *Scomberomorus* specimens are young of *S. sierra*. The information pertaining to these collections is summarized in Table 1. Also included in the table are data kindly provided by other scientists, as well as

published data. The geographical distribution of the catches, all of which originated from coastal waters, is shown in Figure 1.

An 11-mm *S. sierra* collected off Punta Foca, Peru in January 1956 is illustrated in Figure 2. The head, with its long snout, and the large jaws beset with numerous teeth are characteristic of young *sierra* at this stage and serve to distinguish it readily from other scombroids of similar size. Juvenile *Scomberomorus* are also

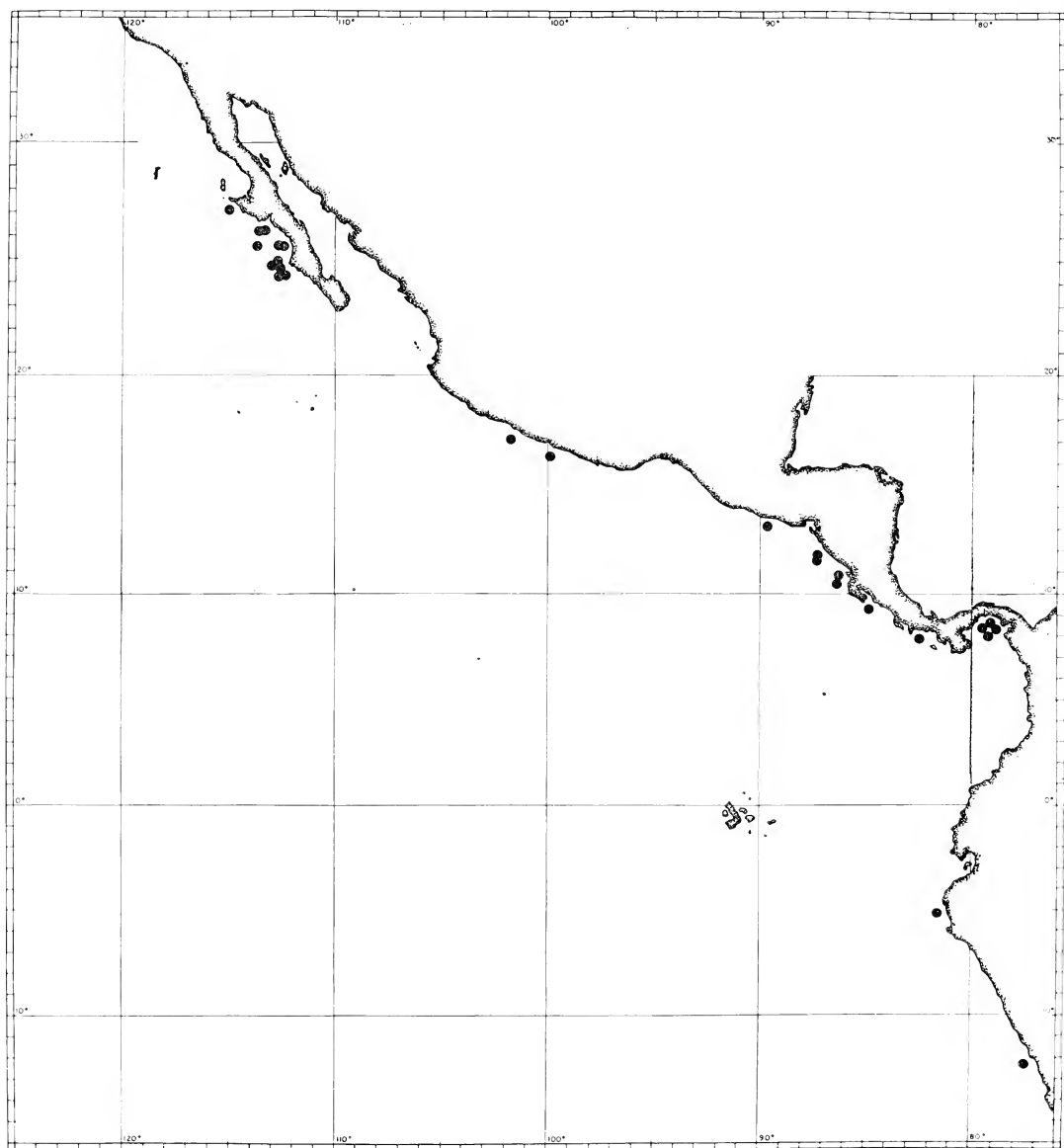


FIG. 1. Localities of capture of juvenile *Scomberomorus sierra* in the eastern Pacific Ocean.

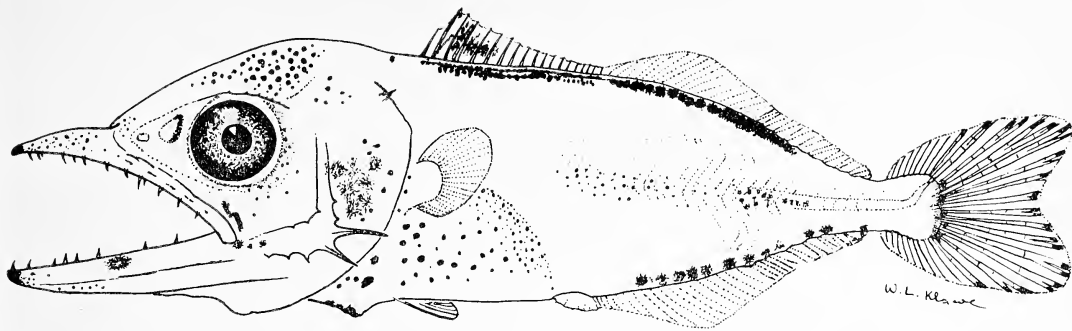


FIG. 2. *Scomberomorus sierra*, 11 mm-long specimen, caught off Punta Foca, Peru.

easily separable from other tuna and tuna-like fishes on the basis of shape, meristic counts, and pigmentation patterns. Noteworthy is the arrangement of head spines illustrated in Figure 3, which represents the dorsal aspect of the head of a specimen 12 mm long from the collection off Punta Foca, Peru. The serrated supraorbital crest shown in that figure is, in the family Scombridae, not restricted only to young of *S. sierra*. Such a crest has been reported for young *Sarda chiliensis* (Pinkas, 1961). Perhaps it may be characteristic of some other members of the family Scombridae phylogenetically closer to the families of Istiophoridae and Xiphiidae, which are considered to be evolved from the scombrids. Young swordfish, marlins, and sailfish at a certain stage of their development are provided with a serrated supraorbital crest. Such a serrated crest is also present in young Gempylidae. *Scomberomorus* and *Acanthocybium* share with the gempylids a cartilaginous projection surmounting the mandibular symphysis (Strasburg, 1964). The appearance of the specimens of young *S. sierra* agrees with the detailed description given by Hildebrand and Cable (1938) for *S. maculatus* and that of Eckles (1949) for *S. sierra*.

Although the number of gill rakers on the first gill arch is useful in separating adults of the two species of *Scomberomorus* found in the eastern Pacific Ocean, young *Scomberomorus* do not have an entire complement of fully developed gill rakers. The full complement is present in individuals on young scombroids (*Thunnus*, *Euthynnus*, *Auxis*, and *Sarda*) of 40–60 mm in total length (Klawe and Shimada, 1959; Klawe, 1961). Counts were made on the

material in this report to establish species identity and the size at which the full complement of gill rakers is attained. Counts of gill rakers made on juvenile scombroids are to a certain extent subjective because, in the smaller individuals, the gill rakers are represented merely as small protuberances along the arch. Because of this subjectivity it is necessary to be wary when comparing counts on young scombroids made by different investigators. From the counts of the total number of gill rakers (Fig. 4), we may assume that the fish in this collection belong to one species because the increase in the number of gill rakers with the increase in size appears to follow a curve which levels off at a size between about 30–50 mm. This leveling off occurs at a number of gill rakers characteristic for *S. sierra*.

It is likely that the Peruvian specimen (Fig. 2) is but a few days old, in view of the rapid growth of young *sierra* noted by Clemens (1956) in his experiments. The fact that still smaller (9.5 mm) specimens of *S. sierra* were also captured at the same time and in the same area suggests that the spawning of *S. sierra* takes place in this region in January. From the summary of the records of capture of juvenile *sierra* (Table 1), this species probably spawns near the coast over most of its distributional limits in the eastern Pacific Ocean. Spawning off Mexico takes place in July, August, and September, and in lower latitudes perhaps from December through April. The conclusions as to time of spawning should be considered as speculative; the question of the spawning time of *sierra* cannot be resolved until more complete data on the occurrence of eggs or young

stages or both come to hand, or until research on the seasonal development of the gonads is carried out.

ACKNOWLEDGMENTS

This report is possible only because many individuals and institutions were willing to provide me with the material and data on which this study is based. Their cooperation is gratefully acknowledged. I am particularly grateful to Dr. E. H. Ahlstrom for loaning the specimens from plankton tows made by the staff members of the organization now known as the California Current Resources of the United States Bureau of Commercial Fisheries. My special thanks go to Mr. Harold B. Clemens, California State Fisheries Laboratory, San Pedro, California. Mr. Clemens not only provided the numerous specimens and the data gathered by him and his colleagues but also contributed to this paper by discussing the subject with me at various stages of preparation of the manuscript.

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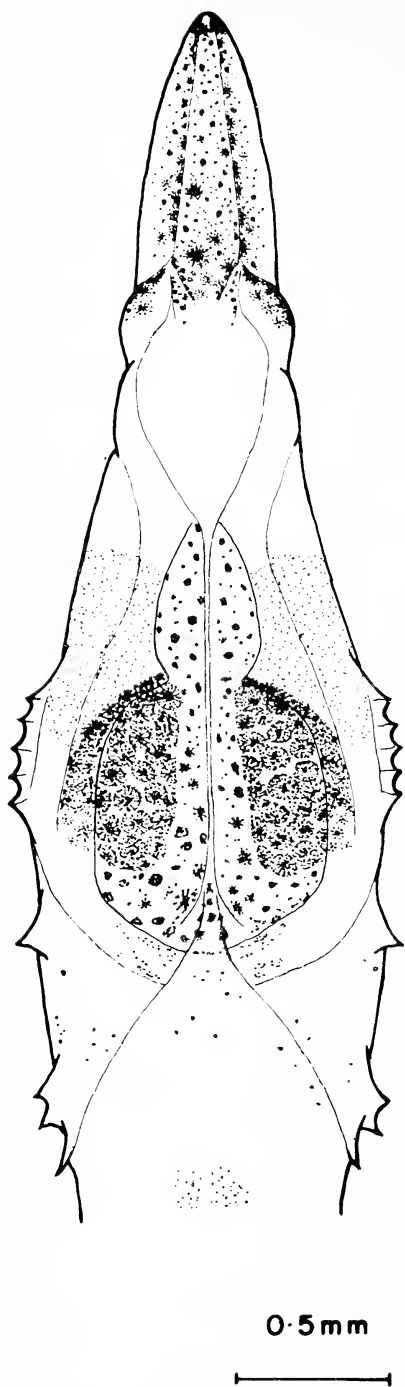


FIG. 3. *Scomberomorus sierra*, 12 mm long; dorsal view of the head. Specimen caught off Punta Foca, Peru.

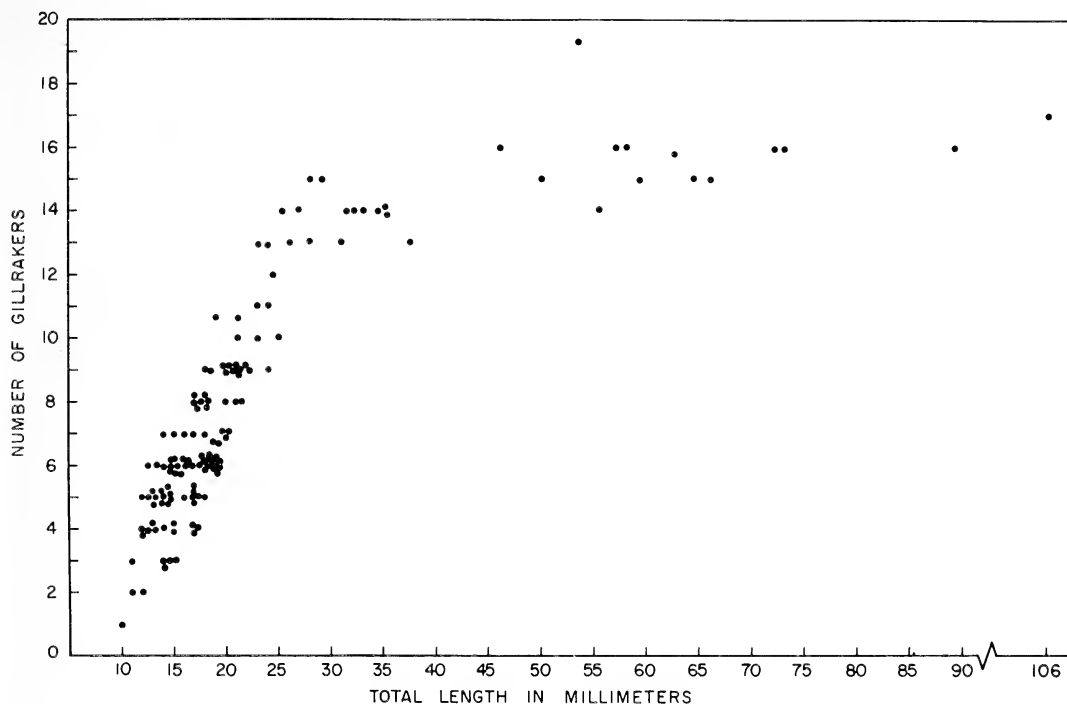


FIG. 4. Gill raker counts of young *Scomberomorus sierra* plotted against total length.

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An Investigation of the Palatability of Some Marine Invertebrates to Four Species of Fish

ELEANOR RUSSELL¹

IN THE PAST, fish attractants have aroused attention, and "bait" extracts have been made which attract fish and excite them to feeding activity (Bateson, 1890; van Weel, 1952; and Steven, 1959).

Less work has been done on repellent substances, apart from shark repellents such as copper acetate (Whitley and Payne, 1947). The repelling action of copper acetate may be due to acetic acid, and it has long been known that dilute acids are repellent to fish (Bateson, 1890, confirmed by Hiatt, Naughton, and Matthews, 1953).

Fish accept eagerly some animal baits while completely ignoring others. On this basis, different degrees of "palatability" ranging to "unpalatability" might be postulated. Among known unpalatable animals there are no obvious common factors with regard to colour or shape, and this suggests that unpalatability is based on the chemical senses.

Many soft-bodied invertebrates are openly exposed to fish attack, and even in the absence of obvious protective devices remain unmolested. Some workers (Garstang, 1890*a, b*; Bullock, 1955; Thompson and Slinn, 1959; Thompson, 1960*a*) have shown that certain marine animals make themselves distasteful to predators by the secretion of diffusible "repellent" substances.

The present investigation was undertaken to obtain data on the relative attractiveness to fish of a diversity of marine animals in southern Queensland. Comparisons of food preferences were made, following in principle the methods of earlier work by Stephenson and Grant (1957) and Blaxter and Holliday (1958).

ACKNOWLEDGMENTS

The author wishes to thank Professor W. Stephenson of the Zoology Department, University of Queensland, who first suggested this problem, and who read the manuscript and suggested many improvements. Thanks are also due to Dr. R. Endean for many valuable suggestions. The work was supported from research funds of the University of Queensland.

GENERAL METHODS

Test Animals

Two marine species, *Pelates quadrilineatus* (Bloch), trumpeter, and *Torquigener hamiltoni* (Gray and Richardson), toado; and two freshwater species, *Gambusia affinis* Baird and Girard, and *Carassius auratus* (L.), goldfish, were used. *Carassius* was obtained from a dealer and the other three species were netted when required.

Freshwater species were used as a control against the familiarity of marine species with invertebrates of their own environment.

Aquarium Conditions

Two glass aquaria (61 × 30.5 × 30.5 cm) without sand were used for each species. Weed was excluded because fish may eat it. Approximately 20 mussels, *Trichomya hirsutes* (Lamarck), were kept in each marine aquarium to remove sediment. Aeration was continuous and salinities were checked weekly. Sizes of the fish, their dietary types, and numbers in aquaria are given in Table 1.

Maintenance Feeding

Fish began eating after a few days and were maintained on prawn, *Metapenaeus mastersii* (Haswell). Each day food was dropped on the

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water. Particles were seized before they reached the bottom.

A known amount of food was introduced, and the amount remaining uneaten after 2 hr was removed and weighed after excess water was removed. This gave a rough measure of the amount of food to be fed each day. Table 1 gives food consumption in gm/gm fish/week.

Testing Methods

Feeding trials were made each day before normal feeding. During tests less normal food (prawn) was given to allow for other food eaten. Only two or three unpalatable materials could be tested in one series of tests, i.e. within 1 hr. If more were tested, the fish ignored even normally palatable material for 3–4 hr.

Comparisons of palatability were made by dropping simultaneously two equal-sized fragments on the water's surface as distant from the fish as possible. As soon as the particles hit the water, the fish swam towards them. Usually both particles were falling through the water by the time the fish reached them. The reaction of the fish to each fragment was observed, and an estimate made of which was preferred. The size of pieces used was that most suitable for the species (see Experiment I). Tests were repeated twice where possible, with an interval of at least one day between tests.

Anticipatory responses were soon evident

whenever a person approached an aquarium. This was particularly so with *Gambusia* and *Carassius*. It was considered that this response would not affect the results: while the initial attraction was visual, final acceptance depended on other factors.

EXPERIMENT I

GENERAL REACTIONS TO INTRODUCED MATERIAL

The reactions of each species to one palatable material (*Metapenaeus*), and to one "neutral," inedible material (plastic tubing) was tested. The significance of different particle size for later tests of palatability was noted.

Results

Gambusia reacted to a large piece of *Metapenaeus* by clustering densely round it and biting at it vigorously for up to 30 minutes. Fragments less than 4 mm across were eaten too rapidly by one or two fish to allow proper classification of palatability.

Gambusia investigated briefly anything dropped into the water. They swam up to a piece of plastic tubing, bit at it a few times, and then let it fall to the bottom where it was ignored.

Carassius swallowed immediately small fragments (less than 4 mm across) of any material.

TABLE 1
DETAILS OF TEST ANIMALS EMPLOYED

SPECIES	SIZE OF FISH (cm)	DIETARY TYPE	AQUARIUM DENSITY: NO. OF FISH PER TANK	AMOUNT OF FOOD NORMALLY GIVEN/WEEK
<i>Gambusia</i>	2.5–3.5	omnivorous	20–30	0.03 gm/gm
<i>Carassius</i>	5–6	omnivorous (Suyehiro, 1942)	4–6	0.035 gm/gm
<i>Pelates</i>	6–9	no published data; omnivorous in aquaria.	4–6	0.2 gm/gm
<i>Torquigener</i>	6–9	no published record; omnivorous in aquaria. Suyehiro (1942) records two related spp. as omnivorous.	4–6	0.2 gm/gm

Small pieces of material such as plastic tubing were rejected some time later. The time of retention was so variable that large fragments were always given for palatability tests. *Carassius* continued to suck at a large piece of *Metapenaeus* for up to 30 minutes. They sucked at a large piece of plastic tubing for up to 20 seconds and then ignored it.

Pelates and *Torquigener* rapidly tore up large pieces of *Metapenaeus*. They bit at large pieces of plastic tubing once or twice and then ignored them. Small pieces were sometimes swallowed and ejected later, so large pieces were always used for tests of palatability.

Any material allowed to remain on the floor of the tank was investigated from time to time by all fish.

EXPERIMENT II

COMPARISONS OF PALATABILITY

Fragments of the tissues of a number of marine invertebrates were fed directly to fish in the comparison situation described above. Tissue of unknown palatability was compared with a known tissue. The initial standard was *Metapenaeus*, but when this proved to be more highly palatable than any other tissue tried, a less palatable substandard was adopted, *Pyrasus ebeninus* Brugière (whelk). The palatability of tissue from 48 different species was tested in this way. Because of the subjectivity of the method, three levels of palatability have been defined on the basis of the reactions of each fish to different types of material. Each material has been assigned to a particular level, rather than placed on an absolute scale.

Results

Three levels of palatability have been defined on the basis of palatability comparisons:

(1) Highly palatable (++) material was always eaten very rapidly by *Pelates* and *Torquigener*, with no preliminary sampling. *Gambusia* and *Carassius* clustered about the material and continued to tear pieces from it for more than 10 minutes and up to 30 minutes.

(2) Palatable (+) material was sampled for a short time before being eaten by *Pelates* and *Torquigener*. *Gambusia* and *Carassius* clustered about the material and tore pieces from it for

a much shorter time, less than 10 minutes, and generally less than 5 minutes.

(3) Unpalatable (0) material was not eaten, but the fish investigated it and often mouthed at it. Differences in degree of unpalatability were noticed: some material was swallowed and later ejected, some material was never swallowed.

Table 2 lists the palatability of all materials tested in this experiment. Minor differences between the four fish in the position of test materials on a nominal scale were not considered significant. There were no differences in the assignment of materials tested to any level of palatability.

Table 3 shows all materials, classed as palatable and unpalatable, grouped with respect to colour. A chi-squared test (Siegel, 1956) shows that the differences in colour distribution between palatable and unpalatable are significant ($\chi^2 = 16.57$, $P < .001$).

EXPERIMENT III

COMPARISONS OF PALATABILITY WHEN TEXTURE AND CHARACTERISTIC APPEARANCE ARE DISGUISED

In Experiment II, no examples of unpalatability were found where appearance was obviously responsible (since all materials were "tasted" before being rejected), but texture was believed to be of some importance. For these tests 13 unpalatable animals were selected to determine palatability after texture was disguised and general appearance was altered.

A solution of gelatin in sea water was used as a base material to which test materials were added. A final concentration of 20% gelatin produced a gel stiff enough to be cut into small pieces which dissolved only slowly in water. The reaction of the fish to gelatin was the same as their reaction to plastic tubing. A homogenate of *Metapenaeus* was added in concentrations of 10–50% to render the whole palatable. A concentration of 10% (by weight) of *Metapenaeus* was sufficient to make the gelatin block highly palatable, and the reaction to 10% *Metapenaeus* was indistinguishable from the reaction to 50% *Metapenaeus*.

Tissues for testing were stored in a deep freeze after collection, and ground in a blender.

TABLE 2
RELATIVE PALATABILITY TO FISH OF ORGANISMS TESTED

MATERIAL TESTED	NO. OF TRIALS	PART OF ANIMAL USED	<i>Gambusia</i>	<i>Carassius</i>	<i>Pelates</i>	<i>Torquigener</i>
CRUSTACEA						
<i>Metapenaeus mastersii</i> (Haswell)	721	tail muscle	++	++	++	++
<i>Callinassa australiensis</i> Dana	1	tail muscle	++	++	++	++
<i>Mictyris longicarpus</i> Latreille	2	leg muscle	++	++	++	++
<i>Alpheus</i> sp.	2	tail muscle	+	+	+	+
ANNELIDA						
<i>Marphysa sanguinea</i> (Montagu)	4	body segments	++	++	++	++
<i>Onuphis ieres</i> (Ehlers)	2	body segments	++	++	++	++
<i>Phyllodoce malgremi</i> Cuvier	2	body segments	++	++	++	++
<i>Pheretima</i> sp.	3	body segments	++	++	++	++
<i>Thelepus setosus</i> (Quatrefages)	3	body segments	+	+	+	+
<i>Thelepus setosus</i> (Quatrefages)	2	tentacles	+	+	+	+
<i>Clymene grossa</i> var. <i>tropica</i> Monro	2	body segments	+	+ → 0	+ → 0	+ → 0
Unidentified terebellid	1	body segments	+	+ → 0	+ → 0	+ → 0
<i>Audouinia tentaculata</i> (Montagu)	3	body segments	0	0	0	0
ECHIUURIDA						
<i>Ochetostoma australis</i> Edmonds	2	body wall	+	+	+	+
SIPUNCULOIDEA						
<i>Phascolosoma dunwichi</i> Edmonds	2	body wall	+	+	+	+
MOLLUSCA						
Lamellibranchiata						
<i>Trichomya hirsutes</i> (Lamarck)	5	mantle	+	+	+	+
<i>Crassostrea commercialis</i> (Iredale & Roughly)	4	mantle	+	+	+	+
Cephalopoda						
Squid	2	muscle	+	+	+	+
Gastropoda						
<i>Uber plumbeum</i> Lamarck	3	foot	+	+	+	+
<i>Pyræzus ebeninus</i> Brugiere	10	foot	+	+	+	+
<i>Nassarius luridus</i> (Gould)	4	foot	+	+	+	+

The organisms tested are arranged according to animal group. Within groups they are arranged in approximate order of palatability.

TABLE 2 (Continued)

MATERIAL TESTED	NO. OF TRIALS	PART OF ANIMAL USED	<i>Gambusia</i>	<i>Carassius</i>	<i>Pelates</i>	<i>Torquigener</i>
<i>Nerita chameleon</i> Linn.	2	foot	+	+	+	+
<i>Austrocochlea obtusa</i> (Dillwyn)	1	foot	+	+	+	+
Opisthobranchiata						
<i>Phyllidea pustulosa</i> Cuvier	2	foot	0	0	0	0
<i>Onchidina australis</i> Semper	2	foot	0	0	0	0
<i>Glossodoris festiva</i> (Adams)	4	foot	0	0	0	0
<i>Aplysia angasi</i> (Sowerby)	3	foot	0	0	0	0
<i>Dolabella</i> sp.	13	foot	0	0	0	0
<i>Notarchus leachii</i> Blainville	4	foot	0	0	0	0
<i>Umbraculum sinicum</i> Gmelin	2	foot	0	0	0	0
BRACHIOPODA						
<i>Lingula bancrofti</i> Johnston and Hirshfeld	2	"stem"	+	+	+	+
	2	body	+	+	+	+
BRYOZOA						
Red colonial	2	part of whole body	0	0	0	0
ECHINODERMATA						
Asteroidea	3	arms and tub. feet	+	+	+	+
<i>Anthenea</i> sp.	2	hepato-pancreas and gonads	+	+	+	+
HOLOTHUROIDEA						
Holothuroidea						
<i>Holothuria scabra</i> Jager	2	body wall	0	0	0	0
<i>Holothuria leucospilota</i> (Brandt)	3	body wall	0	0	0	0
<i>Holothuria pardalis</i> Selenka	2	body wall	0	0	0	0
NEMERTEA						
Black, with yellow stripe	2	part of whole body	0	0	0	0
PORIFERA						
Yellow	1	part of whole body	0	0	0	0
Black	2	part of whole body	0	0	0	0
COELENTERATA						
<i>Alcyonium</i> sp.	5	part of whole body	0	0	0	0
Blue soft coral (fam. Xenidae)	2	part of whole body	0	0	0	0
Sea Pen	1	part of whole body	0	0	0	0

TABLE 2 (Continued)

MATERIAL TESTED	NO. OF TRIALS	PART OF ANIMAL USED	<i>Gambusia</i>	<i>Carassius</i>	<i>Pelates</i>	<i>Torquigener</i>
<i>Catostylus mosaicus</i>	2	homogenate of whole	0	0	0	0
<i>Cerianthus</i> sp.	3	base	0	0	0	0
	3	tentacles of live animal	0	0	0	0
	2	tentacles of dead animal	0	0	0	0
Other anemone	1	tentacles of dead animal	0	0	0	0
ENTEROPNEUSTA						
<i>Glossobalanus</i> sp.	4	anterior part of body	0	0	0	0
PISCES						
<i>Sillago maculata</i>	2	muscle	0	0	0	0
Quoy & Gaimard						
<i>Torquigener hamiltoni</i> (Gray & Richardson)	3	muscle	0	0	0	0

In the preparation of gelatin-base mixtures, a mixed homogenate of *Metapenaeus* and of test tissue was combined with an equal weight of 40% gelatin in sea water to give a final concentration of 20% gelatin. *Metapenaeus* + test tissue mixtures were made in the following proportions:

METAPENAEUS	TEST TISSUE	FINAL CONC. OF TEST TISSUE (%)
5 parts	0 parts	0
4 parts	1 part	10
3 parts	2 parts	20
2 parts	3 parts	30
1 part	4 parts	40
0 parts	5 parts	50

(A criticism of this method is that the concentration of *Metapenaeus* alters as well as that of the test tissue. But if the *Metapenaeus* concentration is kept constant, the total concentration of tissue, and therefore of texture, is altered.)

Within each series, tests were made to find the concentration of test tissue required to make the whole unpalatable. This was checked by comparison with the concentrations above and

below. Tests of different parts or secretions of some animals were also made in this way.

Results

Table 4 lists the animals tested and the concentration necessary to make the mixture of prawn and gelatin unpalatable. Materials are arranged in three groups; the difference between the two "slightly unpalatable" animals and the others is probably real, but the significance of the difference in effect between concentrations of 20% and 30% of test tissue could be questioned.

In no case was there any noticeable difference in palatability between different parts of an animal. When the fresh purple ink of the opisthobranchs *Notarchus* and *Dolabella* was introduced into the fish tanks, the fish swam towards it and through it, often biting at local higher concentrations.

EXPERIMENT IV

SURFACE pH

Thompson and Slinn (1959) and Thompson (1960a, b) have shown that some molluscs produce a defensive acid external secretion

which renders them unattractive to fish. Since the five molluscs tested in Experiment III were all highly unpalatable, their surface pH when alive was measured, and that of all the other animals which were tested in Experiment III.

Universal pH paper was used to measure the normal surface pH after the animal had been placed in a glass dish and allowed to drain for five minutes. Then the surface was wiped with a filter paper, stimulated gently with a glass rod, and the pH ions remeasured.

Results

The surface pH in all cases was approximately 7.0. This result by no means rules out the possibility of acid secretion, but continuous acid secretion and secretion after gentle disturbance are unlikely.

DISCUSSION

Of 48 species tested, the 24 which were unpalatable to fish came from a wide range of animal groups.

It is difficult to compare these results in detail with those of other workers. Stephenson and Grant (1957) worked on *Plectroplites ambiguus* (Richardson), and marine molluscs occupied an equivalent position in the preference scale. However, marine Crustacea were less attractive for *Plectroplites* than were some

marine molluscs, and the most attractive foods for *Plectroplites* (freshwater crustaceans and squid) were relatively less palatable in the present investigation.

Steven (1959) compared the relative effectiveness of natural food substances in evoking exploratory feeding behaviour in *Hepsitia stipes* (Muller and Tröschel) and in *Bathystoma rimator* (Jordan and Swain). Extracts of fresh plankton and of the muscle of the bivalve *Arca zebra* were effective, while the echinoids *Diadema antillarum* and *Lytechinus variegatus* and a holothurian, *Holothuria* sp., also produced intense responses from less extreme dilutions. In the present work certain species of *Holothuria* were found to be unpalatable to fish. However, the presentation of a very small amount of food material, whether palatable or unpalatable (e.g., *Holothuria*), caused exploratory feeding reactions which lasted for one to two minutes.

Three main factors could influence unpalatability: (1) "taste" due to diffusible chemical substances; (2) texture (though not unattractive, the organism may be hard or tough, or may contain spicules); (3) colour, either in itself, or due to association with some other unpleasantness.

In Experiment III, it was shown that unpalatable animals remained unpalatable when the texture was completely altered, and colour to some extent was altered. If colour was the sole cause of unpalatability, fish would ignore food of some particular colour without going near it or taking it into their mouths. Results indicate that this is not generally so; and, while Table 3 indicates that differences in colour between palatable and unpalatable animals are significant, there must be other factors contributing to unpalatability.

Many sedentary, soft-bodied, "unprotected" animals are unpalatable, and these include Porifera, Coelenterata, Nemertea, some Polychaeta, Opisthobranchiata, and Holothuroidea. Many of these animals have no obvious protective devices: *Holothuria scabra* is just as unpalatable as *H. leucospilota*, but has no Cuvierian tubules; a few opisthobranchs eject purple ink, but many do not. Porifera and Nemertea have no obvious physical means of

TABLE 3
EFFECT OF COLOUR ON PALATABILITY:
RELATION BETWEEN COLOUR AND DEGREE OF
PALATABILITY

COLOUR	HIGHLY PALATABLE AND PALATABLE (NUMBER)	UNPALATABLE (NUMBER)
White)	14	2
Grey)		
Cream)		
Red)	8	13
Yellow)		
Orange)		
Brown)		
Blue)	3	5
Green)		
Purple)		
Black	0	3

TABLE 4
TESTS OF PALATABILITY WHEN TEXTURE AND COLOUR ARE MASKED BY GELATIN

GROUP	TEST SPECIES	PART OF BODY TESTED	CONCENTRATION
			NECESSARY TO MAKE GELATIN PLUS PRAWN UNPALATABLE
1 (Slightly unpalatable)	<i>Clymene</i>	whole animal	50%
	<i>Cirratulus</i>	whole animal	50%
2 (Unpalatable)	<i>Torquigener</i>	muscle	30%
	<i>Holothuria</i>	whole animal	30%
	<i>pardalis</i>	cuvierian tubule	30%
	Black sponge	whole animal	30%
		mucus from surface	30%
	<i>Catostylus</i>	whole animal	30%
	<i>Alcyonium</i> sp.	whole animal	30%
3 (Highly unpalatable)	Nemertine	whole animal	20%
	<i>Glossodoris</i>	whole animal	20%
	<i>Aplysia</i>	mantle and foot	20%
	<i>Notarchus</i>	mantle and foot	20%
	<i>Dolabella</i>	mantle and foot	20%
	<i>Umbraculum</i>	mantle and foot	20%

protection, although the texture of a sponge may be sufficient protection.

The most unpalatable animal seemed to be the pleurobranch *Umbraculum*, which most fish did not touch. McNae (1962) notes that "when handled the animal (*Umbraculum*) gives off a characteristic scent reminiscent of that of aplysiids. This scent may have some defensive function." The author has noted a characteristic odour in many opisthobranchs, notably *Aplysia* and *Glossodoris*.

Thompson and Slinn (1959) noted an acid secretion which was apparently responsible for making *Pleurobranchus* distasteful to predators. They recorded that the predators "tasted" but discarded it immediately and, in the case of fish, often violently. Although *Pleurobranchus* is brightly coloured, this did not seem to warn the fish in any way.

In the present experiments, animals with bright, supposedly warning, colouration remained unpalatable when their pattern was destroyed and their colour partly masked by gelatin and *Metapenaeus*. Some cryptically coloured, well camouflaged animals were also unpalatable, notably *Dolabella*, *Notarchus*, *Aplysia*, *Holothuria scabra*, and *H. pardalis*.

These experiments and those of Thompson (1960*a, b*) do not support the idea which seems to have originated with Herdman (1890*a, b*), Garstang (1889, 1890), and Crossland (1911) that cryptically coloured, camouflaged animals were acceptable to fish as food, while brightly coloured ones were rejected because of their warning colouration.

While the results point to the importance of chemical defense mechanisms, the presence of an acid secretion does not seem to be the cause of unpalatability in any of the animals whose external pH was measured. Of all the gastropods tested by Thompson (1960*b*), only five produced an acid secretion, while the remainder had similar glands in the epidermis which produced a secretion which presumably also had a defensive function. In this connection, one must mention the "characteristic odour" of *Umbraculum*, *Aplysia*, and *Dolabella*.

The complex phenomena of learning must play some part in the selection of food by fish, and it is at this level that colour may be important, but learning cannot determine the causes of unpalatability. It is suggested that chemical defense mechanisms may be widespread among invertebrates and that a search

for these, in addition to more obvious mechanisms, would be rewarding.

SUMMARY

1. The palatability of 48 species of marine invertebrates has been determined, of which 24 species were found to be unpalatable to the four test species of fish.

2. There is a significant difference in colour distribution between palatable and unpalatable tissues.

3. Unpalatability remained when texture, colour pattern, and to some extent colour, were masked by presenting the tissue in a gelatin base.

4. It is suggested that chemical defense mechanisms are widespread among invertebrates, and an important factor in determining what fish eat.

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Visual Target Discrimination in Blacktip Sharks (*Carcharhinus melanopterus*) and Grey Sharks (*C. menisorrh*)¹

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CONDITIONED RESPONSE experiments with juvenile blacktip (*Carcharhinus melanopterus*) and grey (*C. menisorrh*) sharks (Schultz et al., 1953) were conducted at the Eniwetok Marine Biological Laboratory, Marshall Islands, during 1960. Our objective was to investigate the sharks' visual capabilities with regard to orientation, form, differential brightness, and color discrimination of targets.

The conditioned response technique has been used only recently in the investigation of sensory perception in sharks. It was employed in auditory studies by Vilstrup (1951), Kritzler and Wood (1961), Olla (1962), Davies et al. (1963), and Wisby et al. (1964), in olfactory studies by Teichmann and Teichmann (1959), in electrical sensitivity studies by Dijkgraaf and Kalmijn (1963), and in visual studies by Clark (1959, 1961, and 1963). Clark's work on instrumental conditioning of lemon sharks is particularly pertinent to the present study.

Related studies on the anatomy and physiology of the visual system of elasmobranchs (Franz, 1913 and 1931; Verrier, 1929; Gilbert, 1963) and behavioral studies in the field (Hobson, 1963) have provided some information on the visual capabilities of sharks. However, with the exception of Clark's work, subjective methods utilizing training techniques have not been used to investigate vision in sharks.

MATERIALS AND METHODS

Subjects

The sharks used were immature blacktips and greys 19 to 33 inches in total length (Table

1) captured from reef flats adjacent to the laboratory.

Experimental Apparatus

The experimental tank was located within a larger rectangular concrete tank which could be subdivided into 5-ft sections (Tester, 1963). It was housed in a building which excluded most light, and some extraneous noise. A booth adjacent to the tank enabled the observer to view the sharks through a narrow slit 5 ft above the water without being seen by them.

The design of the experimental tank is shown in Figure 1, A. Dimensions were: width 4 ft, length 20 ft, and depth 3 ft. The ends were rounded with curved vertical sheets of galvanized iron. Boundaries of the end compartments consisted of notches on the walls and dark lines on the bottom. All sides and ends were painted dull black, but the bottom was brown.

A 6-inch square aperture was cut in the middle of each galvanized sheet, 12 inches below the water level. For some experiments a second square was cut with its upper edge 3 inches below the bottom edge of the first aperture. Targets were mounted on panels which, guided by grooves located behind the apertures, were manipulated from the observation booth by means of cord and pulleys. In successive discrimination training, a single aperture was used. Two targets were clipped together, one above the other, and changes were made by lowering or raising the appropriate target to the level of the aperture. When two apertures were used, in simultaneous discrimination training, three targets were clipped in series, so that the middle and either the top or bottom targets were visible through the apertures.

Paired electrodes were placed along the walls of both end sections *L* and *R*. Each electrode consisted of a brass rod to which were welded nine heavy copper wires spaced 6 inches apart, extending from the surface to within 3 inches

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TABLE 1
CODE NUMBER, TOTAL LENGTH, AND SEX OF
BLACKTIP (B) AND GREY (G) SHARKS

NO.	LENGTH (INCHES)	LENGTH (CM)	SEX
B1	20½	52	F
B2	21	53	F
B3	23	58	M
B4	21¼	54	M
B5	32½	82	M
B6	30½	77	F
B7	22½	57	F
B8	19	48	F
G1	31	79	M
G2	33	84	F

of the bottom. Shocking was accomplished by capacitor discharge. A coupling transformer isolated the system from the 115 volt AC line. Voltage was controlled by a Variac transformer. A fullwave selenium rectifier produced DC which charged a bank of capacitors. The charge was released by a toggle switch controlling a solenoid switch, the latter with heavy contact points. A double-pole, double-throw knife switch enabled the selection of electrode pairs at either end of the tank. The best field was produced at a charge of 90 volts, the maximum ratings of the capacitors.

Visual cues were made of Munsell color standards⁴ on high gloss paper, possessing known values of hue (color), value (brightness), and chroma (saturation), based on the human eye in air.⁵

All targets had an area of 9 sq inches, and consisted of white (N9/) squares, circles, equilateral triangles, and rectangles (1.8 × 5 inches), grey squares with values ranging from white (N9/) to black (N1/), and colored squares with the following characteristics: red (5R5/14), yellow (5Y5/6), green (5G5/8), blue (5B5/6), and purple (5P5/9.2). All colored targets were equal to medium grey (N5/) in subjective brightness for the average human eye. The targets were glued to panels

⁴ Munsell Color Company, Inc., 2441 North Calvert Street, Baltimore 18, Maryland, U.S.A.

⁵ A complete description of the system of specifying color, with graphs for conversion to other systems, is given by the American Society for Testing Materials (ASTM Standards, Part 8, 1958).

of vinyl floor tile which had been painted dull black.

Continuous illumination was provided by a fluorescent light fixture, located about 6 ft above the center of the tank with its long axis parallel to that of the tank. Similar fixtures elsewhere in the shark house contributed only slightly to the illumination, which was measured with a Weston Illumination Meter (Model 756) with Viscor filter. The remote-measurement paddle was housed in a waterproof plexiglass covering. Incident light, measured 1 inch above the water surface at various points of the tank (Figure 1,B), ranged from 27 to 42 ft-c. At any point, the values varied only about 1 ft-c between day and night readings. Measurements taken below the surface of the water (1, 10, and 18 inches) showed vertical gradients from 37 to 30 ft-c in the center of the middle sections, and from 24 to 22 ft-c in the center of the end sections. At the level of the targets and immediately adjacent to them, the illumination was 11 ft-c. The light and water clarity were sufficient to allow a submerged diver with a face plate to distinguish all shapes and colors of targets from one end of the tank to the other.

Training and Testing Procedure

Sharks were trained to associate selected targets with electric shock. This was accomplished by the following procedure:

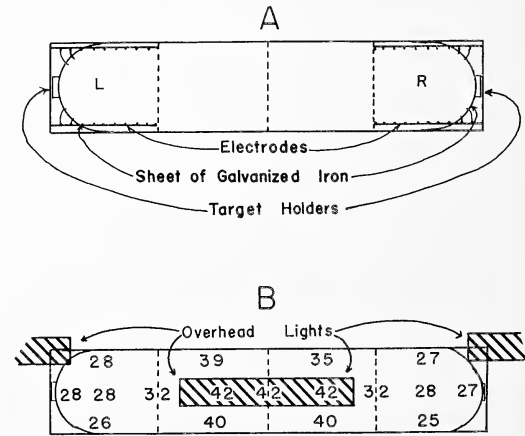


FIG. 1. A, Experimental tank, B, incident illumination one inch above the surface of the water, in foot-candles.

1. The neutral targets were displayed at both ends and the shark was allowed to acclimate.

2. The negative target was displayed at one end for a period of 3 min, and the shark was shocked each time it entered that end.

3. After a rest period of 3–5 min, during which the neutral targets were displayed at both ends, the procedure was repeated at the other end of the tank.

Each training session lasted from 36 to 45 min with six alternating shocking and rest periods, or 18 min of potential exposure to shock. A minimum of 2 hr was allowed between sessions. Training was continued until a shark displayed that it had made the required association, at which time a test was conducted. If after a reasonable number of training sessions the shark had not displayed signs of discrimination, training was discontinued, usually after tests had been conducted.

During test periods the negative target was displayed but no shock was administered when the shark entered the negative end.

Both simultaneous and successive discrimination training techniques (Sutherland, 1962) were employed. In the former case two neutral targets were presented, one above the other, during rest periods, one of which was replaced by a negative target during training.

Criteria of Discrimination

Abrupt changes in behavior, when occurring consistently with appropriate target changes, were considered to be end points of behavior indicating that the shark had made the desired associations, and hence discrimination between the negative and neutral targets. The following are such behavioral changes, one or several of which occurred with individual sharks: (1) head-shaking or body-quivering on facing the negative target for the first time at the start of a training period or during a test period; (2) a sudden swirl or an abrupt change of swimming pattern on presentation of the negative target; (3) turning from the negative target before being shocked, either consistently or at least during the first few passes of each training period, or during test periods; (4) following this behavior, entering the end zone

immediately after the negative target had been replaced by the neutral target; (5) sudden dashes into and out of the negative end zone immediately after the target was displayed; (6) dashing toward the negative target and abruptly turning at the line marking the entrance; (7) abrupt decrease in excitability when the target was changed to neutral, or abrupt increase in excitability when the negative target was presented.

RESULTS

Using the criteria listed above, sharks were subjectively judged to have succeeded or failed to discriminate between negative and neutral targets. Results of all experiments are summarized in Table 2; the total training time (including shocking but not control periods) and number of training sessions are entered in Table 3. In cases of positive conclusion, the times and sessions represent training until discrimination was evident. In all such cases additional training confirmed the results.

Some sharks (marked ? in Table 2) displayed good signs that they could discriminate, but their over-all behavior was too erratic to afford a firm conclusion. The implication is that further training might possibly have strengthened the association.

Behavior During Training

When a shark was shocked as it entered the end zone displaying the negative target, its body twitched noticeably. Usually it would dash away from the end compartment (escape response). Often, however, depending on the particular shark and its experience at being shocked, it would continue into the end zone despite the shock, and would turn either at the end or at some intermediate point.

During training, most sharks first developed an end association, i.e., after one or more shocks during a training period, they learned which end produced punishment and either avoided that end for the remainder of the period or, before penetrating it, displayed signs such as head-shaking which showed the end = punishment association. With most sharks, end association developed into target association with

TABLE 2

RESULTS OF DISCRIMINATION TESTS WITH BLACKTIP (B) AND GREY (G) SHARKS

(+ = discrimination; ? = probable discrimination; 0 = no discrimination;

* = simultaneous discrimination problems)

TARGETS (NEUTRAL VS. NEGATIVE)	SHARKS									
	B1	B2	B3	B4	B5	B6	B7	B8	G1	G2
No target vs. white triangle	+	—	—	—	—	—	—	—	—	—
White horizontal vs. white vertical rectangle	—	—	+	+	+	+	—	—	+	—
White square vs. white triangle	?	+	—	—	—	—	—	—	—	—
White circle vs. white triangle	—	—	—	0	?	—	—	—	+	—
Grey (N5/) square vs. purple square	—	—	—	—	0*	—	—	—	—	—
Grey (N5/) square vs. blue square	—	—	—	—	?	—	—	?	—	—
Grey (N5/) square vs. green square	—	—	0	—	—	—	—	?	0	—
Grey (N5/) square vs. yellow square	—	—	—	—	—	—	—	+	—	0*
Grey (N5/) square vs. red square	—	—	—	—	—	—	?	+	—	?
Grey (N5/) square vs. grey (N6/) square	—	—	0	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N8/) square	—	—	+	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N6/) square	—	—	+	—	—	—	—	—	—	—
Grey (N5/) square vs. grey (N8/) square	—	—	—	—	—	—	—	0*	—	+

further training. This was shown by one or more kinds of overt responses, such as head-shaking, on seeing the negative target when displayed at either end. The criteria of discrimination have already been listed.

It was expected that learning of the target = punishment association would be followed, with further training, by learning to avoid the end zone in which the negative target was displayed (avoidance response). The avoidance response was learned reasonably well (with tests showing 0–10% of the total end-zone passes into the negative end) by only two sharks in apparently simple problems: B1, no target vs. target; and B3, horizontal vs. vertical rectangles. It was not learned by other sharks trained to the rectangle orientation problem, nor by those exposed to discrimination problems involving squares, circles, triangles, colors, and shades of grey.

Prolonged training in attempts to induce the avoidance response sometimes produced behavior which might be classed as negativistic or "rebellious," e.g., with B5. This blacktip had undergone extensive training to the circle vs. triangle problem with some signs of discrimination. During rest periods, it would circle quietly in the center zone. At the start of a training period, it would make an initial shal-

low pass into the end displaying the negative target, turn back and enter the neutral end, and then dash into the negative end with head shaking and body quivering.

Some blacktips (but not grey sharks) had initially, or developed during training, a tendency to circle between the center zone and one end zone. This was called an "L-bias" or an "R-bias," depending on which side was favored. Two sharks (B1 and B6) showed an L-bias during shape discrimination experiments; four (B3, B5, B7, and B8) developed a strong R-bias during color discrimination experiments. The end bias could not be overcome by persistent shocking nor, in the following instance, by offering food as a reward. B6 was being trained to distinguish between horizontal and vertical rectangles but showed persistent penetration of the L-end and avoidance of the R-end. At 1845 hours, during a rest period a piece of fish was put into the R-end, upstream of L, to induce the shark to enter. It approached the R-end with seeming interest but did not enter. At 2010 hours, while being consistently shocked at L as it entered against the negative target, it suddenly dashed into the R-end, took the fish, and then dashed back into the L-end to be shocked again as it entered.

Some blacktips displayed behavior which

might be termed "nervousness," particularly in problems involving grey vs. colored targets and, to a lesser extent, in problems involving squares, circles, and triangles. This was manifested by a hypersensitivity to incidental noises which normally did not seem to affect the sharks but which, with prolonged training, caused them to make sudden dashes and quick turns. Other signs of nervous activity were: (1) apparent agitation and rapid circling, (2) prolonged figure-8 oscillations against the wall of the tank, or (3) rapid dashes from one end of the tank to the other during which the shark would turn on its back and rub the floor. This last behavior may have been related to irritation from the tag or from copepod parasites on the back which was further aggravated by body-twitching induced by shocking. A similar behavior was occasionally seen in sharks which were not being conditioned.

In most discrimination problems, the black-

tips circled with increased frequency in the safe center zone as training proceeded, thus avoiding shock at either end. This circling tendency slowed the training process and in a few cases caused us to abandon training temporarily or permanently. It did not occur with the grey sharks.

There was no noticeable difference in response between sharks subject to successive and simultaneous training techniques. Each method was used in about half of the total number of test situations (Table 2).

Despite the behavioral problems discussed above, some sharks did learn to discriminate between targets. The results are presented in the sections which follow.

No Target versus Target

The one shark (B1) presented with this problem learned to associate the target (white triangle) with shock after 36 reinforcements

TABLE 3
TIME (IN MINUTES) OF TRAINING AND NUMBER OF TRAINING SESSIONS (IN PARENTHESES),
FOR BLACKTIP (B) AND GREY (G) SHARKS

TARGETS (NEUTRAL VS. NEGATIVE)	SHARKS									
	B1	B2	B3	B4	B5	B6	B7	B8	G1	G2
No target vs. white triangle	36 (2)	—	—	—	—	—	—	—	—	—
White horizontal vs. white rectangle	—	—	72 (4)	158 (11)	122 (10)	72 (4)	—	—	54 (3)	—
White square vs. white triangle	360 (19)	320 (19)	—	—	—	—	—	—	—	—
White circle vs. white triangle	—	—	—	78 (5)	486 (27)	—	—	—	180 (10)	—
Grey (N5/) square vs. purple square	—	—	—	—	180 (10)	—	—	—	—	—
Grey (N5/) square vs. blue square	—	—	—	—	108 (6)	—	—	144 (9)	—	—
Grey (N5/) square vs. green square	—	—	204 (15)	—	—	—	—	255 (18)	198 (11)	—
Grey (N5/) square vs. yellow square	—	—	—	—	—	—	—	18 (1)	—	198 (11)
Grey (N5/) square vs. red square	—	—	—	—	—	—	360 (20)	89 (5)	—	210 (12)
Grey (N5/) square vs. grey (N6/) square	—	—	108 (6)	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N8/) square	—	—	108 (6)	—	—	—	—	—	—	—
Grey (N5/) square vs. grey (N8/) square	—	—	—	—	—	—	—	96 (9)	—	216 (12)

in two training sessions. Training was continued for three more days (24 sessions, 438 min) during which time B1 consistently demonstrated that it had learned the association. In addition, it also learned to avoid the negative area with almost perfect performance.

Orientation and Form Discrimination

WHITE HORIZONTAL VS. VERTICAL RECTANGLE: Discrimination of orientation of rectangles was demonstrated by all sharks, four blacktips and one grey, presented with this problem. In training sessions extending over 1–3 days, clear signs of discrimination were shown after the following number of reinforcements: B3–127; B4–365; B5–609; B6–138; G1–120. In all cases, continued training and tests provided consistent evidence that the sharks could discriminate.

Among the blacktips, B3 and B6 with the faster rates of learning were fresh sharks which had not been trained previously, whereas B4 and B5 with the slower rates had been trained unsuccessfully to the apparently difficult circle-triangle problem (see below). The grey shark, with the fastest rate of learning, had previously been trained successfully to the circle-triangle problem.

Only B3 learned to avoid the negative end. It retained the discrimination for at least 18 days without reinforcement. A gradual extinction of the association of the negative target with shock was apparent in tests conducted after 7, 12, and 18 days without reinforcement.

WHITE SQUARE VS. TRIANGLE: Two blacktips were exposed to this problem with uncertain success in one (B1) and certain success in the other (B2). Neither shark had prior training experience.

B1 showed occasional signs of discrimination after 362 reinforcements (8 sessions in 3 days), but its behavior was too erratic to afford a firm conclusion, even after an additional 11 training sessions and a total of 629 reinforcements.

An initial attempt at training B2, involving 375 reinforcements (14 sessions in 3 days), was unsuccessful. When training was resumed after 4 days of rest, a sudden and obvious development of the association was apparent after 68 reinforcements (5 sessions). Continued

training confirmed the positive conclusion. Tests of retention after 5 days without reinforcement were inconclusive.

WHITE CIRCLE VS. TRIANGLE: Of three sharks presented with this problem, one (B4) failed to discriminate, another (B5) showed inconsistent signs of discrimination, and the third (G1) made the discrimination.

After 103 reinforcements in 5 sessions, B4 started to swim continuously in the center zone. Training was terminated because of the persistence of this behavior.

After 727 reinforcements (17 sessions in 3 days), B5 showed some signs of discrimination. However, an additional 305 reinforcements (10 sessions in 2 days) failed to provide further evidence.

The grey shark (G1) was trained successfully to discriminate between the circle and triangle after 476 reinforcements (10 sessions in 2 days), but it did not learn the avoidance response, even after an additional 12 sessions (216 min, 380 reinforcements in 2 days).

Color Discrimination

The training of blacktips to discriminate between grey and colored squares of the same subjective brightness (to the human eye) seemed to produce more hypersensitive and erratic behavior than was displayed in other discrimination problems. It was clear that some of the subjects discriminated between the targets, but no adequate attempt was made (by substituting different shades of grey) to determine if the discrimination was based on differential brightness or hue per se.

GREY VS. PURPLE: One shark (B5) presented with this problem failed to show any sign of discrimination after 611 reinforcements during 10 sessions in 2 days.

GREY VS. BLUE: Both of two blacktips presented with this problem showed infrequent signs of discrimination, but in neither case was it possible to reach a firm conclusion.

B5 had apparently not made the discrimination after 358 reinforcements (6 sessions in 1 day). However, two tests conducted after a period of rest provided some evidence that it could distinguish between the targets.

B8 was subjected to 2 days of training dur-

ing which time it received 282 reinforcements in 9 sessions. Although it showed many signs of discrimination during training periods, tests failed to verify the positive conclusion.

GREY VS. GREEN: One blacktip (B3) and a grey shark (G1) failed to discriminate this combination, but a second blacktip (B8) showed some indications of discrimination.

B3 received 299 reinforcements (15 sessions in 2 days), while G1 received 424 (11 sessions in 2 days).

B8 showed several signs of discrimination during training (18 sessions in 3 days, with 417 reinforcements). However, tests failed to confirm a positive conclusion.

GREY VS. YELLOW: A grey shark (G2) presented with this problem failed to discriminate whereas a blacktip (B8) showed clear signs of discrimination.

G2 underwent 11 training sessions in 2 days, receiving 483 reinforcements without showing any signs of learning.

B8 showed that it could discriminate from the first of 6 training sessions (total of 155 reinforcements, 99 min) conducted in 1 day, and in a test conducted the following day. The rapid rate of learning suggests that stimulus generalization had occurred. B8 had been trained to the grey-green combination prior to training against yellow.

GREY VS. RED: Of three sharks presented with this problem, a grey (G2) and a blacktip (B7) showed only inconsistent signs of discrimination, but a second blacktip (B8) definitely made the discrimination.

G2 underwent 12 training sessions in 2 days, receiving 434 reinforcements. Occasional signs of discrimination were shown during training and concluding tests, but no decision was possible because of inconsistent behavior.

After an initial 2 days of training (13 sessions, 362 reinforcements) B7 showed some signs of discrimination. However, tests failed to confirm the conclusion. An additional day of training with 166 reinforcements in 7 sessions failed to produce more definite signs of discrimination.

In contrast, B8 showed definitely that it could discriminate after 86 reinforcements in 5 sessions. An additional 6 sessions (108 min,

189 reinforcements) and concluding tests left no doubt of discrimination.

Brightness Discrimination

Experiments on differential brightness were conducted with two blacktips (B3 and B8) and one grey shark (G2). One blacktip (B3) demonstrated the ability to distinguish between shades of grey differing by 2 Munsell units, and the grey shark discriminated a difference of 3 Munsell units.

When trained to distinguish between N5/ and N6/, B3 showed no signs of discrimination after 6 sessions over 2 days (117 reinforcements). In 6 sessions of the following day (171 reinforcements) it was then successfully trained to distinguish between N4/ and N8/. A test confirmed the positive conclusion. Another test, conducted after an additional 4 training sessions (42 reinforcements) left no doubt of discrimination. When N6/ was substituted for N8/ following the last test, it was found that stimulus generalization had occurred, and B3 reacted to N6/. However, it did not respond similarly to N5/ which was also substituted for N8/, giving a difference of only 1 Munsell unit.

B8 showed no signs of discrimination between N5/ and N8/ after 9 sessions (2 days) and 196 reinforcements.

G2 showed inconsistent signs of discrimination between N5/ and N8/ during 12 training sessions in 2 days, involving 473 reinforcements. Tests confirmed that it could discriminate. Substitution of N6/ for N8/ produced some signs of discrimination, but no firm conclusion was possible.

DISCUSSION

Training Technique and Learning

The principal aim of our training technique was to induce sharks to avoid the shocking area when they had learned to discriminate the negative target, thus producing a quantitative measure of response based on the number of passes into the neutral and negative zones. In preliminary experiments conducted in 1959, some of which involved training tanks and tech-

niques of different design, blacktips were readily trained to avoid the negative end, especially with "easy" problems, e.g., no target vs. target, and small vs. large white targets. In the results reported here, only two sharks learned the avoidance response, and only in the apparently simple problems of no target vs. target and rectangle orientation.

Difficulty in inducing avoidance may have been due partly to the lack of obvious visual cues marking the entrance to the punishment area, such as would be provided by a partition with an opening or by a barrier in a "shuttle box" such as that used by Wodinsky et al. (1962). Another factor may have been our technique of exhibiting the negative target for prolonged periods rather than single displays. Preliminary experiments indicated that the former method, although it complicated the learning process by first developing an association with the negative *end* of the tank rather than with the target itself, still resulted in faster learning of the required associations than the latter method.

Another factor of considerable importance is the use of electric shock as an aversive stimulus. Church (1963) reporting upon the varied effects of punishment on behavior, points out that electric shock may elicit a variety of responses, including avoidance and aggression.

Since some subjects learned to avoid the shock in addition to discriminating the targets in simple problems, it seems likely that their failure in other problems may have been due to the fact that the problems were bordering on the threshold of the shark's visual capabilities. This may also account for the heightened activity and hypersensitivity which resulted after continued training to "difficult" problems. Such behavior occurred frequently, making it difficult to assess visual capabilities and often forcing postponement or termination of training.

There was also a suggestion that the sharks' performance may have been influenced by prior training experience. After blacktips had been trained unsuccessfully with difficult or impossible problems, they showed a relatively slow rate of learning when later presented with easier problems, e.g., orientation of rectangles.

With continued training in attempts to de-

velop the avoidance response, some blacktips exhibited an apparent attraction for the shock. Their behavior indicated that the punishment was anticipated, and, once shocked, they often persisted in the negative zone despite repeated shocks. Best (1963) notes a somewhat similar behavior exhibited by planaria subjected to instrumental conditioning. After having demonstrated that they could make the required choice, their performance deteriorated as they chose the unrewarded alternative and became lethargic. He notes that higher animals, particularly cats, frequently exhibit such behavior, even choosing to lie on an electric grid and receive the shock rather than attempt to avoid it. He also states that "most workers agree that it may be due to overpunishment and . . . some kind of emotional response toward the entire test situation." The behavior of blacktips, and, to a lesser extent, of grey sharks, can probably be attributed to an emotional response caused by extensive punishment in training them to difficult or perhaps impossible discrimination problems.

Visual Capabilities

It has generally been assumed that the shark eye is adapted for high sensitivity rather than acuity because of its rod-rich retina, high ratio of rods to ganglion cells, and the presence of a reflecting tapetum (Gilbert, 1963). Absence of cones in vertebrate eyes is usually correlated with poor retinal resolution and colorless vision, although Walls (1942) points out the possibility that cones may not be the sole mediators of color vision. Cones have been reported to be absent in most shark retinas examined (Walls, 1942). Recently, however, Gruber et al. (1963) found for the first time some cones in a carcharhinid shark, *Negaprion brevirostris*, and in two species of *Carcharhinus* as well. In a histological study of blacktip retinas, Kato (1962) found only a single type of visual cell, presumably the rod, despite an intensive search for a second type. He also found a high ratio of visual cells to ganglion cells. A few grey shark retinas examined were similar (unpublished). Both retinas, then, are adapted for sensitivity rather than acuity. The behavior of captive sharks indicated that they could perceive small

targets from a distance of at least 5 ft and sometimes at about 10 ft, supporting the histological conclusion of high sensitivity.

Regarding form discrimination, Sutherland (1962) reports that no particular difficulties in discrimination between squares, circles, and triangles have been encountered in most animals that have been tested, including octopuses, minnows, sticklebacks, pike, and a variety of higher animals. However, he points out that the angle of rotation of the figure was frequently important; for example, he found that with octopuses, a normal square (with horizontal base as in our tests) and an equilateral triangle were easier to discriminate than a diamond (square rotated through 45°) and an equilateral triangle.

Clark (1959) successfully trained two large lemon sharks (*Negaprion brevirostris*) to associate a 16 inch square white target with food. Three nurse sharks (*Ginglymostoma cirratum*), however, failed to make a strong association. Clark (1961, 1963) also trained lemon sharks to distinguish between a square and a diamond, and between a plain white square and one with vertical stripes, but was unable to train them to discriminate a square from a circle even with the large targets used.

Our blacktips and greys readily discriminated between rectangles oriented at 90° to each other. However, in other test situations involving circle vs. triangle and square vs. triangle, only two of five sharks provided positive results. The shark's difficulty in form discrimination may be attributed to poor retinal resolution, or possibly to differential ability in learning, which, in turn, may be related to our methods. Hobson (1963) suggests that form discrimination may not be utilized by grey sharks in their natural environment. In feeding tests, he found no significant discrimination between whole baitfish (suitably slit to provide good olfactory stimulation) and decharacterized baitfish (heads and fins removed).

Clark (1961, 1963) trained lemon sharks to distinguish between a white and a red circle, and a white and a red square. As in our experiments, the luminosity factor was not eliminated.

In our tests with blacktip and grey sharks,

some subjects were able to distinguish, but with apparent difficulty, red and yellow, and possibly green and blue also, from grey targets. As indicated above, it still remains a question as to whether the sharks were responding to differences in brightness or to hue. The colors were chosen for maximum chroma and, to the human eye, presented a vivid contrast with grey when viewed through water. Although the illumination was somewhat low, measuring 28 ft-c at the surface and 11 ft-c at the level of the targets, there was enough light to allow color vision, at least for animals with cone-rich retinas that have demonstrated the ability to distinguish hues. For humans, 0.01 ft-c is sufficient for photopic vision (Moon, 1961). Walls (1942) reports several workers' findings that the minnow *Phoxinus laevis* matches human ability in regard to the illumination level at which they can perceive hues. John (1964), utilizing schooling responses of *Astyanax mexicanus*, found a cone threshold in the order of 0.001 ft-c.

Eyes of blacktips and greys kept in the shark house were nearly in a completely light-adapted state: the pupils were almost slits, and the tapeta were nearly completely occluded by dark pigment. It is possible that a small increase in illumination might have raised the sharks' visual ability, as it would certainly have done for animals with duplex retinas. However, optimum light conditions for blacktip and grey sharks, with all-rod retinas, may not necessarily be the same as those of animals with cone-rich retinas.

There was no noticeable difference in learning rates or ability between the simultaneous and successive techniques employed. It has been shown (Sutherland, 1962) that the former method is more advantageous if very small differences, such as neighboring shades of grey, are to be discriminated. Using the simultaneous technique, shades of grey differing by 3 Munsell units were distinguished by a grey shark but not by a blacktip. Using the successive technique, shades of grey differing by 2 Munsell units were distinguished by a second blacktip.

Difference Between Species

No consistent differences were found in the visual capabilities of blacktip and grey sharks.

However, there was a difference in their response to punishment. While undergoing training, blacktips frequently displayed hypersensitive and erratic behavior, while grey sharks did not deviate much from their normal swimming pattern. This may reflect a real difference in normal behavior. Hobson (1963) found that blacktips were much more wary than grey sharks in their natural environment.

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Body Temperatures of Malaysian Rain Forest Mammals

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ABSTRACT: Rectal temperatures of 23 species of Malaysian mammals were recorded during the course of an intensive mark-recapture program in rain forest. Repeated capture allowed repetitive readings for many individuals over several months. Individual variations and group comparisons are tabulated and discussed. Comparisons are made with body temperatures of arctic and temperate mammals. It was concluded that mean temperature for all tropical mammals described in this study was lower than in higher latitude forms, but that comparisons, to be meaningful, should be restricted to equivalent taxonomic groups.

BODY TEMPERATURES of tropical mammals are poorly known. Most published records refer to single individuals of exotic groups not having counterparts in more northerly latitudes. Often temperature data are taken from animals held in captivity for long periods (particularly in zoos), and the reliability of such data from animals living in captive environments may be questioned. This paper reports the temperatures of 23 species of Malaysian mammals of four orders, many individuals of which were repeatedly captured and on which multiple readings were possible (Table 1).

Rodbard (1950) has suggested that the mean body temperature of mammals weighing less than 1 kg bears a simple and direct proportion to body weight. In an effective refutation, Morrison and Ryser (1952) point to an essentially constant mean body temperature in most mammals. These authors, along with Scholander et al. (1950) and Wislocki and Enders (1935), agree however that certain groups of mammals (notably the monotremes, marsupials, edentates, and chiropterans) either maintain a consistently low body temperature or show a great temperature lability. Moreover, but without supporting data, Morrison and Ryser (1952) point out the possibility that within certain selected homogeneous groups of good regulators body temperatures may be significantly different from the general mammalian norm of 37.8° C. The present paper illustrates such a condition, particularly in the comparisons of 11 species of

sympatric murid rodents and of 4 species of sciurid rodents. Illustrated as well is individual variation in body temperatures and to a lesser extent behavioral relationships to temperature.

MATERIALS AND METHODS

All data derive from a single locality—Ulu Gombak, 20th mile Pahang Road, 1½ mile NE Genting Simpah Youth Hostel, State of Selangor, Malaysia. The elevation at this location is about 1,900 ft. The climate in Malaya (about 3° N) is remarkably constant; the photoperiod varies only about 20 minutes over a year. Humidity and rainfall are generally high, although both daily and "seasonal" variations occur.

With the exception of the bats and of the single bamboo rat all mammals were taken in an area of 14 acres in primary and old secondary rain forest marked off in a trapping grid at intervals of 50 ft. For the entire trapping period (1 November 1963–22 May 1964) 225 live traps were maintained on the ground. In trees at varying heights small platforms were built on which traps were maintained, of which 50 were kept throughout the period and another 25 were added about halfway through. Normally traps were open four nights a week and were baited with coconut meat and banana. Trapped animals were brought each morning to a small shelter on the edge of the grid where temperature and other data were taken. Animals were then toe-clipped for individual identification, if not previously marked, and were returned to the station of capture for release. A total of 29,189 trap nights resulted in the

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capture of 377 individuals of 21 species with a total capture-recapture record of 2,616. Many individuals were recaptured five or more times. To minimize trauma of handling, temperatures were never taken oftener than once a week in frequently captured animals. Normally, however, the vagaries of recapture did not allow for temperature readings oftener than once every three or four weeks. A few additional temperature measurements came from individuals collected away from the grid area.

All temperatures were taken rectally with a Schultheis rapid-recording thermometer read to 0.1° C. Insertion of the entire bulb well past the lip of the column was simple enough for all but the smallest species (*Tylonycteris*). Even so, the temperatures recorded for this small bat are believed to be accurate. Data from obviously ill or moribund animals are not included in Table I. However, where these data might suggest critical temperatures they are included later in the discussion. There was no direct attempt to determine critical temperatures nor to determine metabolic responses to changing ambient temperatures. Confidence limits were calculated only when the sample constituted 10 or more individual readings.

RESULTS AND DISCUSSIONS

Individual Variation

Single healthy individuals irrespective of sex regularly varied within a two or three degree range over long periods of time. Yet the range on the temperature spectrum, while being consistent for individuals, often differed between them. Consistent behavioral differences seemed to correlate well with these individual patterns. The following tabulation shows repeated temperature readings of single individuals over many months. The individuals were selected because their behavior deviated sufficiently from the norm of the species to warrant mention in field notes. Only animals of the same sex and equivalent weights are compared.

Rattus rajah

- ♂ Docile 36.5; 36.5; 35.1; 36.3; 35.5; 36.2; 37.8; 35.9; 36.8; 37.9; 36.4 (\bar{x} = 36.44; r = 35.1–37.9)
 ♂ Aggressive 36.4; 38.7; 38.9; 38.0 (\bar{x} = 38.00; r = 36.4–38.9)

Rattus muelleri

- ♀ Docile 35.0; 35.4; 35.2; 35.8; 36.3 (\bar{x} = 35.56; r = 35.0–36.3)
 ♀ Aggressive 37.8; 37.3; 38.6; 38.1; 38.1; 36.4 (\bar{x} = 37.71; r = 36.4–38.6)

Rattus sabanus

- ♂ Docile 35.3; 36.1; 37.5; 35.2; 34.8; 36.3; 35.3; 37.4; 36.8; 36.5; 37.9 (\bar{x} = 36.28; r = 34.8–37.9)
 ♂ Aggressive 36.6; 36.2; 37.3; 37.8; 37.5; 35.8; 39.2; 39.4; 38.4; 38.3 (\bar{x} = 37.65; r = 35.8–39.4)
 ♀ Docile 36.6; 36.7; 36.8; 36.9; 36.2; 36.3; 34.8; 37.2 (\bar{x} = 36.45; r = 34.8–37.2)
 ♀ Aggressive 35.2; 37.1; 37.4; 35.4; 37.1; 37.3; 36.1; 36.0; 38.0; 37.8; 38.2; 37.9; 38.9 (\bar{x} = 37.10; r = 35.2–38.9)

In these instances mean temperature readings between individuals of like species, sex, and weight varied as much as 1.5° C. Yet, essential consistency characterized the body temperatures of these and most other individuals of groups generally regarded as having a high ability to regulate temperature. Only in one group other than rodents are repeated readings available. In the insectivore *Hylomys* the temperature range in individuals was slightly wider than in most rodents. One adult male with seven readings showed a variation of 2.8° C (33.6°–37.4°); an adult female with eight readings showed a variation of 3.0° (35.1°–38.1°).

The possible influence of the trapping regime on temperature was checked in 16 repeatedly taken individuals of four species of *Rattus*. Since trapping and handling procedures were standardized, it was assumed that individuals captured 20 or more times might become habituated and therefore show less variation in temperature. The first three and the last three temperature readings were graphed against body weight. Although changes in both measures occurred, in no case was there a consistent pattern of temperature change. The range of temperature remained as great after several months of trapping as at the beginning.

Relation of Temperature to Reproductive State and Sex

In the first weeks of trapping a few individuals showed signs of recent lactation. How-

TABLE 1
RECTAL TEMPERATURES OF 23 SPECIES OF MALAYSIAN RAIN FOREST MAMMALS*

SPECIES NAME	NO. OF INDI- VIDUALS	NO. OF TEMP. READINGS	TEMPERATURE RANGE	MEAN \pm 95% CONF. LIMITS	COEFFICIENT OF VARIABILITY
Insectivora					
Erinaceidae					
<i>Hylomys suillus</i>	14	34	33.6–38.1	36.11 \pm 0.35	2.79
<i>Echinosorex gymnura</i>	2	2	28.1–32.3	30.20	—
Chiroptera					
Pteropidae					
<i>Cynopterus brachyotis</i>	3	3	34.0–36.3	35.33	—
Vespertilionidae					
<i>Tylonycteris robustula</i>	9	9	34.3–38.4	36.64	—
Primates					
Tupaïidae					
<i>Tupaia glis</i>	4	9	35.8–39.2	37.50	—
<i>Tupaia minor</i>	2	2	39.1; 39.1	39.1	—
Lorisidae					
<i>Nycticebus coucang</i>	1	1	34.9	34.9	—
Rodentia					
Sciuridae					
<i>Callosciurus caniceps</i>	4	4	40.1–41.4	40.65	—
<i>Callosciurus notatus</i>	6	6	35.8–41.2	38.58	—
<i>Callosciurus nigrovittatus</i>	1	2	40.1; 40.9	40.50	—
<i>Sundasciurus tenuis</i>	10	12	36.6–42.1	39.44 \pm 1.13	4.59
Rhizomyidae					
<i>Rhizomys sumatrensis</i>	1	1	36.1	36.1	—
Muridae					
<i>Rattus annandalei</i>	2	12	36.1–38.2	37.10 \pm 0.63	1.76
<i>Rattus muelleri</i>	26	79	34.5–39.2	37.04 \pm 0.28	3.53
<i>Rattus sabanus</i>	157	670	33.7–39.4	36.54 \pm 0.53	7.61
<i>Rattus rajah</i>	21	86	35.1–39.6	37.25 \pm 0.58	7.32
<i>Rattus surifer</i>	55	138	34.4–39.3	37.40 \pm 0.32	5.32
<i>Rattus jalorensis</i>	6	6	34.8–38.2	36.80	—
<i>Rattus cremoriventer</i>	9	16	36.2–39.7	38.20 \pm 0.40	1.97
<i>Rattus whiteheadi</i>	19	36	35.8–39.2	37.91 \pm 0.28	2.34
<i>Rattus edwardsii</i>	4	20	34.6–38.2	36.22 \pm 0.48	2.89
<i>Rattus bowersi</i>	6	8	34.2–37.5	35.87	—
<i>Chiropodomys gliroides</i>	21	32	35.9–39.1	37.80 \pm 0.35	2.59

* Scientific names follow Harrison and Traub (1950) and Medway (Mammals of Borneo, *in press*).

ever, throughout the majority of the period there was no other evidence of breeding. Therefore temperature readings recorded herein have to be considered applicable to nonbreeding animals.

Sexual differences in temperature were generally very small and were concluded to be insignificant. For this reason no sexual separations are made in Table 1. Curiously, however, in the sibling species pair, *Rattus rajah* and *R. surifer*, females consistently showed higher tem-

peratures. In *R. rajah* mean temperatures of females were 1.3° higher than males; in *R. surifer* 0.5° higher. There is no ready explanation for these differences.

Relation of temperature to body weight

Irving and Krog (1954), Morrison and Ryser (1952), and Scholander et al. (1950) effectively show that mammalian body temperature bears no primary relationship to body weight. Rather consistent differences in tem-

perature relate to the mammalian order and the adaptive habits of the species in question. With the exception of *Nycticebus* all 22 species described in this paper weigh less than 1 kg. Of these only one, *Echinosorex*, regularly exceeds 500 g. Its position as a primitive insectivore prompted me to remove it from comparison with the remaining species. To determine whether consistent temperature differences were apparent among these small mammals, four 125-g categories were created. The temperatures of animals of different species whose adult body size did not exceed 125 g were averaged to constitute the first class; those from 125–250g the second class, and so on. Mean results were as follows: Class I, 37.85°; Class II, 37.41°; Class III, 36.72°; Class IV, 35.87°. The last class included only one species (*R. bowersi*). Only the first class meets the mean value of 37.8° given by Morrison and Ryser (1952) as applicable to most mammals weighing under 1 kg. Differences between means are not as great as temperature differences displayed by individuals over periods of time. Nonetheless, there is a consistent decline in mean temperature as adult animal size increases. Most of the species included in the foregoing classes are rodents. About all one may conclude from these data is that no single figure precisely describes mean temperature values even among phylogenetically closely related forms.

Critical Internal Temperature

In the absence of experimental data critical temperatures can only be estimated by indirect means. Apparently a lowering of 4–5° from normal is the maximum tolerable drop. Records of three subadult male *Rattus sabanus* may illustrate. The first individual was heavily wetted and quiet at first capture but still in apparent good health. At this time its body temperature was 36.4°. In its next three captures the animal was very active and showed a mean temperature of 38.4° (38.0°–38.9°). A second individual, quiet but in good health on its first three captures, had a mean temperature of 35.9° (35.4–36.2). The animal was dry but obviously sickly on its fourth capture and at this time had a temperature of 31.3°. It was not subsequently recaptured. A third individual, heavily wetted and moribund at its first capture, had a body

temperature of 31.4°. At its second capture six days later its temperature was 35.9°.

Comparisons of Groups

The mean temperature of all mammals in this study was 37.1°. Morrison and Ryser (1952) place the mean temperature of 56 species of mammals in the 15 g–700 kg range at 37.8°. Irving and Krog (1954) place the value at 38.6° for 22 species of arctic and subarctic forms. One might postulate a latitudinal relationship with temperature. Since, however, large and consistent differences in temperature exist between groups it seems more reasonable to compare only equivalent taxonomic units. The mean temperatures of five groups are listed below.

Insectivora	(2 sp.)	33.2°
Primates	(3 sp.)	37.2°
Chiroptera	(2 sp.)	36.0°
Rodentia		
Sciuridae	(4 sp.)	39.8°
Muridae	(11 sp.)	37.1°

In these instances it is clear that a single mean value cannot meaningfully represent the "typical" body temperature of a tropical mammal. Moreover, different species within these groups often consistently differ. The two gymnures differ markedly, for example, and both differ from soricine insectivores (Morrison and Ryser, 1952). *Tupaia* has "squirrel-like" temperatures rather than the somewhat lower values found in other primates. The sciurids maintain a consistent "above average" temperature in relation to most mammals (as noted also in Irving and Krog, 1954 and Spector, 1956). Even among murid rodents mean values of the smaller species are 2° higher than the largest (*Rattus bowersi*). The need to consider the adaptive requirements of the particular group seems obvious. How to judge what these adaptive requirements are is, of course, a more difficult task.

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Observations on *Themeda australis*-*Eucalyptus* Savannah in Papua

P. C. HEYLIGERS¹

SAVANNAHS, vegetation types with a ground cover dominated by grasses and an open tree storey, are extensive in the coastal lowlands of the Central District, Territory of Papua (Fig. 1). These lowlands were included in a regional survey carried out in 1962 by a team of the Division of Land Research and Regional Survey, CSIRO.

This paper describes the vegetation of savannah near Jackson's Airport, about 12 km east of Port Moresby. Emphasis is laid on correlation with edaphic conditions. The field work, in cooperation with the geomorphologist and the pedologist of the team, was done in July and August 1963.

The following data pertinent to this area are extracted from the survey report (Mabbutt et al., 1965).

The climate is monsoonal: strong southeasterly winds prevail during the dry season from May till October, in which monthly rainfall averages 30 mm, and light variable winds during the rest of the year with monthly rainfalls averaging 160 mm. Table 1 gives more detailed information about rainfall, together with data on temperature and evaporation.

The landscape, made up of strike ridges and vales, is underlain by fairly steeply dipping rocks of Tertiary age. Cherty shale, marl, and limestone form the rounded ridges; the vales have been cut in less resistant tuff. Relief is in the order of 100 m. Lithosols and regosols are found on the ridges, brown clay soils and texture-contrast soils on the higher parts of the flatter land, and dark clay soils and alluvial soils near and along drainage lines. The vegetation is savannah, predominantly of the *Themeda australis*-*Eucalyptus* type, with tall grass vegetation and forest along permanent streams.

Fires are common throughout the dry season, at the end of which most of the ground cover has been burnt. Regrowth starts after some rain has fallen. Areas burnt early in the dry season can have a fair cover at the end of it and are liable to burn off again. At the time of our investigation, notwithstanding high rainfall in June, the dry season was already well advanced and fire had destroyed the ground vegetation of a part of the area under investigation.

Wild life in the area is very scarce and its influence on the vegetation is negligible. Grazing by cattle is restricted to a few fenced properties.

Two transects were selected for observations: transect 1 was located 3 km south of Jackson's Airport near the Rigo Road; transect 2 about 1.5 km northeast of the airport. Levels were taken along each transect and at selected situations pits were dug, varying in depth between 1.0 and 2.5 m.

TOPOGRAPHIC AND SOILS DESCRIPTION OF THE TRANSECTS

Each transect comprised a fairly straight, smooth hill slope attaining 22° to 30° and with minor rock outcrop, passing into a shallowly dissected foot slope mainly between 0°30' and 5° and up to 1200 m long, and ended at a small strike stream, which on transect 1 has a narrow bordering flood-plain.

Much runoff is as sheet flow: slope wash on hill slopes results in small terracettes, and on foot slopes leaves a fairly abundant lag gravel (Mabbutt and Scott, 1966).

Each transect had a similar sequence of soils (Scott, unpublished data). The hills are occupied by red regosols, which are deeply developed at the lower slope of site 2. On the adjacent foot slopes texture-contrast soils are found, whilst black clay soils occupy the remainder of the flatter country, forming a

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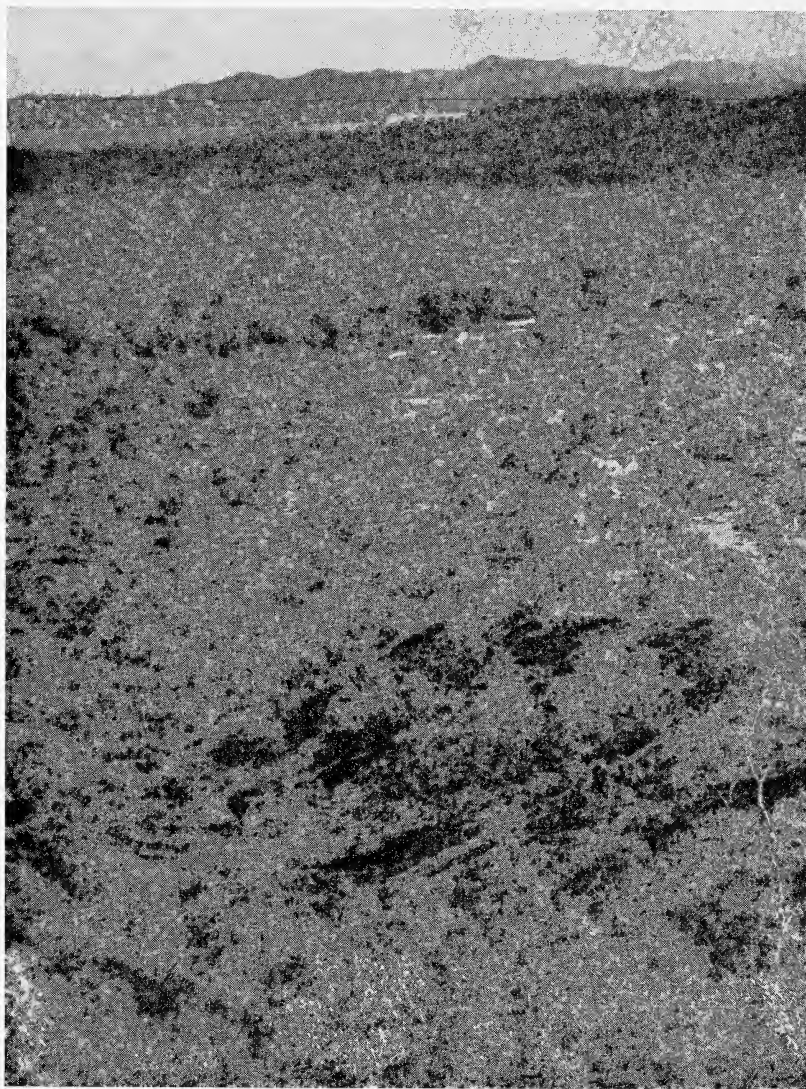


FIG. 1. View from the crest of a strike ridge over the savannah country just east of, but similar to, that in which the transects were laid out. The foothill in the foreground rises fairly abruptly from the foot slopes, which end against a forested narrow flood-plain. In the farther distance is another strike ridge shadowed by clouds and backed by Bootless Inlet.

belt of 50 m width parallel with the creek at transect 1, but extending over 300 m from the gully at transect 2. The soil of the flood-plain is an organic black clay.

THE VEGETATION

The *Themeda australis*-*Eucalyptus* savannah has a tree stratum of one or more of the *Eucalyptus* species *E. alba*, *E. confertiflora*, and

E. papuana, and some scattered *Albizia procera*; and a grass cover dominated by *Themeda australis*, with *Heteropogon contortus* and *Sebima nervosum* commonly associated, the latter especially on stonier soils. A shrub layer is only locally developed; *Albizia procera* and *Cycas media* are the more important species. This type of savannah occurs on both transects, except for a fringe of forest and tall grass on the narrow flood-plain.

The Trees

DISTRIBUTION PATTERNS (Fig. 2): *Eucalyptus alba* occurred over the whole transect 1; its height ranged from 9 to 16 m. On the black clay and adjacent texture-contrast soils it was accompanied or predominated by *E. confertiflora*, of about the same height. Relative proportions of *E. alba* and *E. confertiflora* varied between 6:4 and 2:8. On the rest of the texture-contrast soils and the regosols *E. alba* was joined by *E. papuana*, varying in height between 10 and 20 m and mostly remaining subordinate. Relative proportions varied between 9:1 and 5:5. Somewhere in the central part of the texture-contrast soils, over a distance of about 50 m, an overlap in the area of *E. confertiflora* and of *E. papuana* occurred (Fig. 3). On the transition to the organic black clay soils some specimens of *E. papuana* also occurred.

E. papuana occurred over the whole transect 2, with heights ranging from 10 to 18 m on the flat country and from 17 to 22 m on the slopes and along the gully. *E. alba*, 9–13 m high, was concentrated on the texture-contrast soils, but some trees occurred along the gully and one single tree was growing on the slope. On the texture-contrast soils the relative proportions of *E. alba* and *E. papuana* varied between 8:2 and 5:5. Not a single specimen of *E. confertiflora* was seen.

The density is in the order of 150 trees per hectare. A more exact determination of density was abandoned because of signs of wartime disturbance such as local cutting of trees, trees that were pushed over, and patches of rather dense eucalypt regrowth. Moreover, it is unlikely that this would have contributed very much to an explanation of the described distribution pattern. Observations of the 1962 survey show that this rather haphazard pattern is a general feature. More detailed regional investigations may reveal the causal factors.

ROOT SYSTEMS: Root systems were studied in 11 pits, which had been dug at the foot of the trunks, by removing as much soil from the roots as was possible without undue time-consuming effort. They usually appeared to consist of a small taproot and about five main horizontal roots branching from the base of the

TABLE 1
MEAN MONTHLY TEMPERATURE, RAINFALL, AND EVAPORATION AT JACKSON'S AIRPORT, PORT MORESBY

	JAN.	FEB.	MARCH	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	ANNUAL
Mean max. temp. (°C) *	31.9	31.4	31.3	30.8	29.9	29.1	28.0	27.8	28.7	30.0	31.2	32.0	30.3
Mean temp. (°C) *	28.2	28.0	28.0	27.5	27.0	26.1	25.3	25.3	25.9	26.9	27.7	28.3	27.0
Mean min. temp. (°C) *	24.5	24.4	24.3	23.0	23.9	23.2	22.8	22.7	23.2	23.7	24.3	24.7	23.8
Mean rainfall (mm) *	146	219	144	222	38	15	10	23	65	23	81	159	1139
Rainfall in 1963 (mm) **	322	179	297	75	36	313	40	10					
Mean evaporation (mm) *	161	126	140	119	134	115	141	165	164	210	192	180	1836

* Data from Fitzpatrick (1965).
** Data from monthly statistical summaries of Bureau of Meteorology, Melbourne (for the 8 months preceding this investigation).

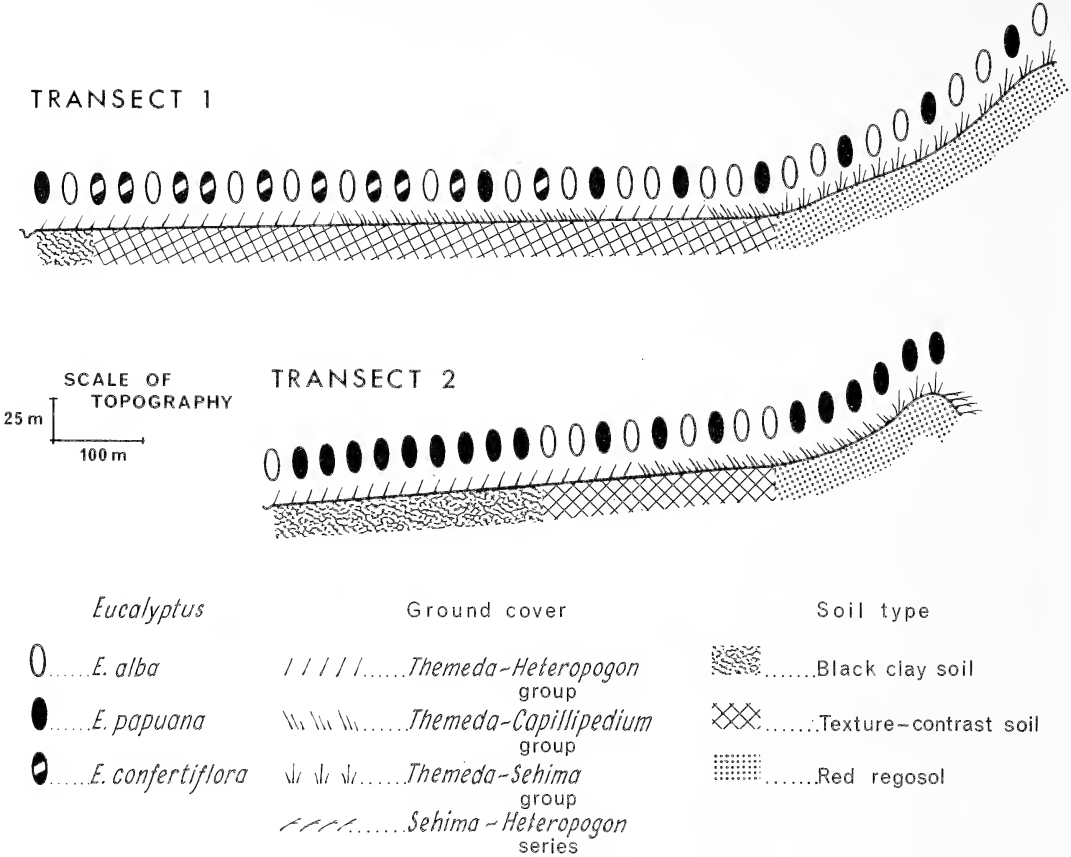


FIG. 2. Diagram of the transects, showing the distribution and mutual proportions of the *Eucalyptus* species, and the distribution of the ground cover groups and of the soil types.

trunk. The horizontal roots of *E. papuana* are often oval in section with the long axis vertical, and divide at or near the base in several horizontal roots above each other (Fig. 4).

Horizontal roots run for distances up to about 25 m more or less parallel with the surface, often not deeper than 0.2 m, only very gradually tapering. Near the base vertical roots branch off from horizontal roots, and are particularly common in some specimens of *E. alba*. In some cases these roots run down vertically more than 1.5 m, but more often they gradually bend away obliquely, and may even bend up and penetrate the topsoil again, where they continue horizontally.

The way in which the main roots of *E. alba* branch off from the base of the trunk is different from that of *E. papuana* and *E. conferti-*

flora, where they gradually emerge from the base. In the case of *E. alba* the trunk is usually a little swollen, but sometimes is considerably so. With a trunk diameter of 24 cm, the diameter of the base may vary between 30 and 45 cm. Just below the surface the base is constricted, under which constriction the main roots branch off.

The taproot, if present, may reach a depth of 1.3 m but is usually shorter. It branches off under acute-angle, thick roots, which show the same features as described above for the vertical roots. One specimen of *E. alba* was found which lacked the cluster of horizontal roots but which had a very stout taproot.

Tree roots with diameters of 1 cm or less, whose origin could not be traced, were found scattered at depths of 1.3 m, and rootlets with

diameters commonly less than 1 mm were still found at a depth of 2 m (bottom of the deepest pits). Rootlets of 1 or 2 mm diameter were seen branching off from the main roots; they have a slightly thickened base.

The conclusion is reached that the *Eucalyptus* species studied have root systems with major roots strongly developed in horizontal directions, rather close to the ground level, and smaller roots penetrating to depths of 2 m and over.

The Shrubs

Except for young specimens of the eucalypts, *Albizia procera* was the only shrub encountered

over the whole length of both transects. It was, however, more common on the flatter parts. Mostly varying in height between 1.5 and 3.5 m, some reached a height of 8 m and thus penetrated into the tree layer. The shrubs grow in clusters and consist mostly of little-branched shoots, which were generally shedding leaves at the time of the investigation. Examination of the surface soil and removal of the superficial soil layers revealed that the shoots are linked by a network of creeping woody rootstocks, often as thick as the base of the shoots (Fig. 5). From the rootstock branch off vertical and oblique roots, which branching does not seem to have any correlation with the places



FIG. 3. The overlapping distribution area on transect 1 of *Eucalyptus confertiflora* (with flaky bark) and *E. papuana* (tree with light trunk and slender foliage at right). The tree at the left (with damaged bark) is *E. alba*. In the foreground several branches of *Albizia procera* shrubs; in the background an area of eucalypt regrowth. The ground cover is formed by the *Themeda*-*Capillipedium* group.



FIG. 4. Root system of *Eucalyptus papuana* in black clay soil of transect 2. (The camera looks obliquely down into the pit.) Under the basal whorl of main horizontal roots a small taproot can be seen, which divides into upward-bending roots.

where the shoots originate. These vertical roots taper rapidly and the deepest penetrations observed were about 0.9 m. From them branch off horizontal and downward rootlets of diameters varying between 1 and 2.5 mm.

Cycas media has its main distribution on the slopes; some specimens, however, were found near gullies and the gallery forest margin. It was completely absent on the intermediate, flatter parts of the transects. Usually *Cycas* remains low, 0.5 or 1 m high, but occasionally it reaches heights of 4 m.

For the sake of completeness the occurrence is mentioned of a few specimens of *Pandanus* sp., *Antidesma ghaesembilla*, *Timonius timon*, and *Desmodium umbellatum*, growing on black clay soil along the gullies and creeks.

The Ground Layer

GENERAL COMPOSITION: The ground layer is composed mainly of grasses, of which

Themeda australis, *Heteropogon contortus*, and *Sehima nervosum* are the commonest; *Capillipedium spicigerum* and *Sorghum nitidum* are subordinate; and *Cymbopogon procerus*, *Dichanthium superciliatum*, *Themeda novoguineensis*, and *Panicum* sp. are occasionally found. The season was not very favourable for the study of other herbs. Some dried sedges were found, of which only *Eleocharis monostachyos* on black clay soils was recognizable. Among the forbs the Papilionaceae were best represented: *Lourea obcordata*, *Crotalaria linifolia*, *Alysicarpus vaginalis*, *Uraria lagopodioides*, *Pycnospora lutescens*, *Tephrosia ?maculata*, and four species not yet identified, of which two were twiners. Among the others were: *Passiflora foetida* (Passifloraceae), *Evolvulus alsinoides* (Convolvulaceae), *Melothria maderaspatana* (Cucurbitaceae), *Tridax procumbens* (Compositae) ?*Borreria* sp. (Rubiaceae), and several Labiatae. Because of the general poor condition



FIG. 5. Root system of *Albizia procera* consisting of rootstocks connecting the trunks and giving anchorage to the shrubs or trees, and of vertical roots scattered along the rootstocks.

of these plants at this time of the year, no attempt has been made to study their distribution.

A feature observed locally at transect 1 and common on transect 2 was a crust of greenish or reddish brown algae, which could cover as much as 20% of the ground. These algae were not restricted to the flatter areas, but occurred also on the slopes. Mosses occurred sparsely and were commonest on the lower slopes.

INFLUENCE ON TERRACETTES: Grass tussocks may play a role in the formation of terracettes, which are especially common on steeper slopes but occasionally can be seen in flatter areas. A number of tussocks form an obstacle to the runoff flow and soil material accumulates at the upslope side. Differences in level at the two sides are mostly a few centimeters, but may become more than a decimeter; factors leading to enlargement of this difference include slope angle, age of tussock, and texture of soil material. Tussocks contribute in this way to

stability of the slopes (Mabbutt, unpublished data).

COMPOSITION OF THE GRASS COVER: The investigation was concentrated on the grasses, which generally were fruiting and therefore had probably reached their maximum production; *Sehima* had already lost most of its inflorescences. The overall height of the grass cover was about 1.1 m on the flat parts of the transects, decreasing to 0.9 m on the slopes. The culms were mostly fairly erect; locally, however, they could be more or less inclined. Foliage cover averaged about 50%, but extreme local variations occurred; almost bare areas could lie next to areas with nearly 100% cover. These changes are related to microtopography—depressions have a more open vegetation—and cover of the soil by grit and gravel, whilst severe disturbance during the war could have been a factor in some of the cases. Trees and shrubs did not seem to have a noticeable influence on the grass cover.

The grass cover was sampled near each of the soil pits and on the steep side of the hill at transect 2. A series of 10 plots was cut along a line at right angles to the direction of the main transect or following the contour, the plots spaced three paces apart. In a few cases burnt areas made a deviation of the scheme necessary. A plot was delineated by a frame of 28.3×70.7 cm, comprising an area of 0.2 m^2 (Figs. 6 and 7). The grasses were cut at about 1 cm above the ground, and the species were kept separately. Some plots seemed to contain also some material from earlier seasons. The samples were dried in sun and wind for several days, keeping them indoors at night, after which they were weighed. At this stage they could still have held up to 10% moisture, but this drying at least made the samples mutually comparable. In addition, in each plot records were made of the total cover of the tussock bases as left after cutting; the number and the diameter of the base of the tussocks per species;

the length of some of the longest culms; and the area covered by leaf litter, algae, grit and gravel, and stones. Moreover, a series of 10 plots gave frequency figures for the species.

The production per series, expressed as the average dry weight per sample plot of 0.2 m^2 , appeared to be very variable and the 95% confidence limits to the means showed that only the series with lowest production significantly differed from the four with highest production. Also, the figures for *Themeda australis*, the only species with consistently high frequency and showing a tendency to increasing production downslope, failed to show significant differences.

Because of these nonsignificant differences, series have been combined in groups, according to the relative importance of the species in the composition of the sward (percentage of species in total dry weight of a series). Three series remained separate because of their strongly deviating composition; the others were in-

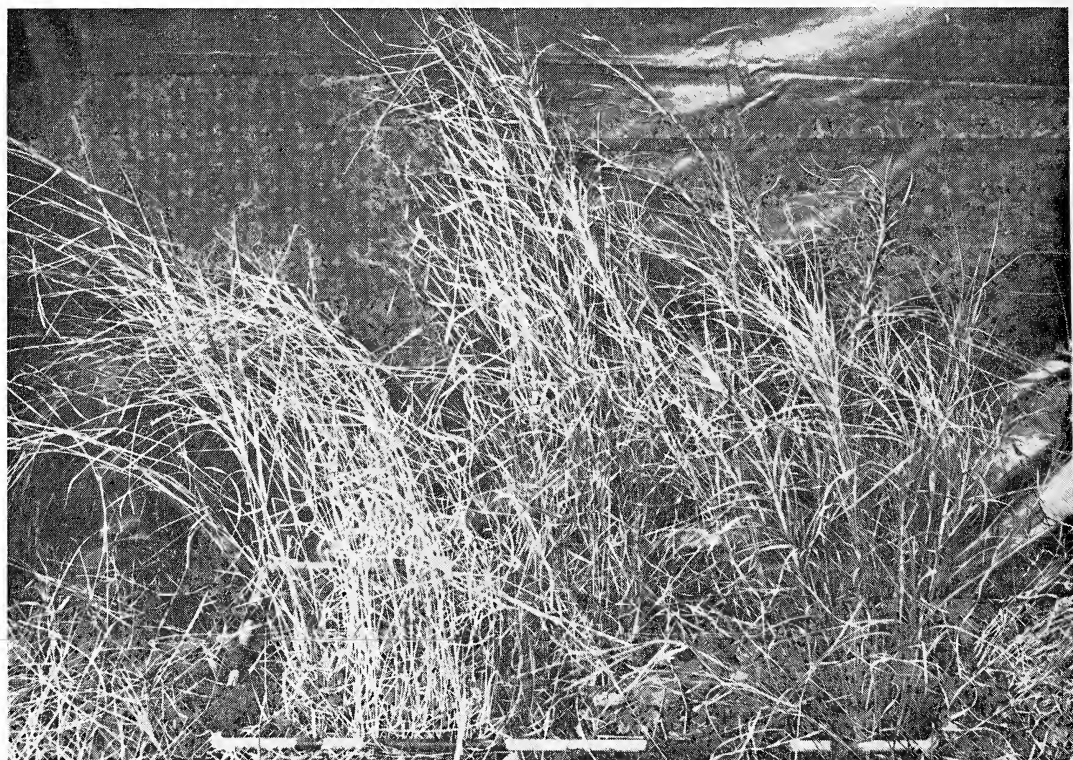


FIG. 6. A plot on the lower hill slope of site 1, containing three and a half tussocks of *Sehima nervosum* (in centre and at left) and one of *Themeda australis* (at right).

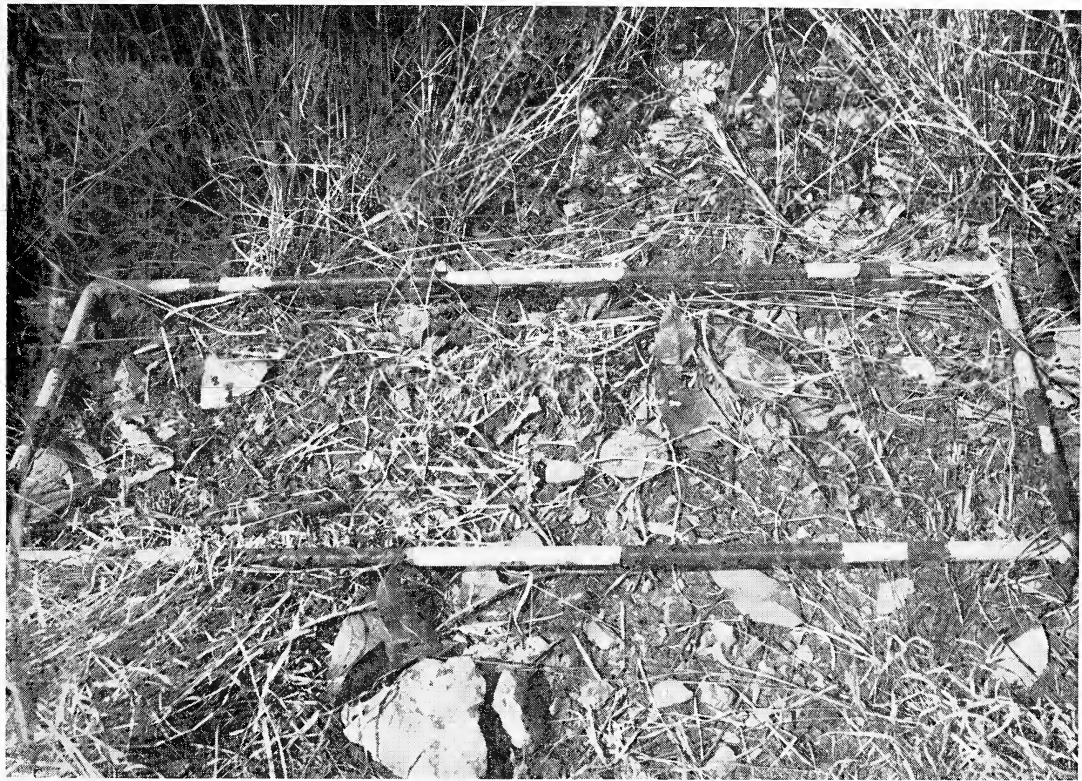


FIG. 7. The same plot after cutting shows the tussock bases, some leaf litter, and scattered gravel. The frame adapted from Daubenmire (1959) comprises an area of 0.2 m² and is painted to divide by sight the area into squares of 10%, 5%, and 2½% to facilitate estimation of cover.

corporated in three groups of 6, 6, and 7 series respectively, called the *Themeda-Heteropogon* group, the *Themeda-Capillipedium* group, and the *Themeda-Sebima* group. The three remaining series are the *Themeda* series, the *Themeda-Sorghum* series, and the *Sebima-Heteropogon* series. Of the three groups the production of the *Themeda-Heteropogon* group and of the *Themeda-Capillipedium* group are not significantly different, but the *Themeda-Sebima* group produces significantly less than the two other groups (Table 2).

Other data on the groups are given in Table 3. There appears to be a good correlation between the composition of the sward by weight and the basal cover of the tussocks. Also, total production and total basal cover show the same correlation. An inverse correlation exists between basal cover of the tussocks and the number of tussocks: with increasing number of tussocks the basal cover decreases, due to the

poorer quality of the tussocks, which is also reflected in the average length of the largest culms.

The *Themeda* series consists of a pure but rather poor stand of *Themeda australis*. The *Themeda-Sorghum* series contains about equal

TABLE 2
TOTAL GRASS PRODUCTION OF THE *Themeda australis-Eucalyptus* SAVANNAH*

GROUP AND SERIES	AVERAGE GRASS PROD. (GM)
<i>Themeda-Heteropogon</i> group	126 ± 17
<i>Themeda-Capillipedium</i> group	115 ± 16
<i>Themeda-Sebima</i> group	81 ± 10
<i>Themeda</i> series	76 ± 32
<i>Themeda-Sorghum</i> series	119 ± 60
<i>Sebima-Heteropogon</i> series	83 ± 18

* Figures give the average production of grass in grams of air-dry matter per plot of 0.2 m², with the 95% confidence limits to the means.

quantities of *Sehima nervosum*, *Sorghum nitidum*, and *Heteropogon contortus*, and double that amount of *Themeda australis*, with a little *Dichanthium supercilium*. The third series, the *Sehima-Heteropogon* series, with a production almost the same as the *Themeda-Sehima* group, consists of about equal quantities of *Heteropogon contortus* and *Sehima nervosum*, with *Themeda australis* accounting for only 6% of the dry matter.

DISTRIBUTION PATTERNS (Fig. 2): The *Themeda-Heteropogon* group occupies the lowest parts of both transects, with slopes varying between 0°30' and 3°, and occurs on black clay soil as well as on texture-contrast soil, the former with a 20 or 30 cm deep crumbly topsoil,

the latter with a crumbly topsoil of only 5 or 10 cm. Deeper layers have a blocky, lenticular, or columnar structure, are black, dark grey, or dark brown, and frequently have calcium carbonate concretions. The pH in upper layers varies between 5.5 and 7.0, and increases at depth to 8.5. Some 20% of the ground is covered by litter, mainly of the eucalypts, and 10% is covered by grit and gravel, both showing a great local variation.

The *Themeda-Capillipedium* group occupies the intermediate parts of the transects. At transect 1 it occurs on texture-contrast soil alternating with the *Themeda-Heteropogon* group, at transect 2 on texture-contrast soil and adjacent regosol; consequently it occurs over

TABLE 3
SPECIFIC DATA OF THE GROUND COVER GROUPS
(T-H = *Themeda-Heteropogon* group; T-C = *Themeda-Capillipedium* group;
T-S = *Themeda-Sehima* group)

	<i>T. australis</i>	<i>H. contortus</i>	<i>C. spicigerum</i>	<i>Sorghum nitidum</i>	<i>Sehima nervosum</i>	OTHER GRASSES	TOTALS
Weight (g/m ²)							
T-H	517	87	10	13	2	—	629
T-C	407	76	78	3	12	1	577
T-S	218	50	3	—	131	4	406
Percentage composition of sward by weight							
T-H	82	14	2	2	—	—	100
T-C	72	13	13	—	2	—	100
T-S	53	12	1	—	33	1	100
Basal cover of tussocks (%)							
T-H	4.05	0.84	0.10	0.06	0.005	—	5.08
T-C	3.24	0.73	0.95	0.01	0.2	0.01	5.02
T-S	1.66	0.54	0.02	—	1.36	0.11	3.67
Percentage areas of tussock bases							
T-H	81	16	2	1	—	—	100
T-C	63	14	19	—	4	—	100
T-S	45	15	—	—	37	3	100
Number of tussocks per m ²							
T-H	14.7	3.4	1.6	0.5	0.2	—	20.4
T-C	15.6	3.1	4.2	0.1	0.3	0.2	23.5
T-S	15.3	4.8	0.7	—	6.9	0.2	27.9
Frequency (%)							
T-H	96	43	10	10	2	—	
T-C	93	33	32	3	7	3	
T-S	84	43	4	—	73	3	
Average length of longest culms (cm)							
T-H	143	111	135	102	95		
T-C	139	111	135	115	95		
T-S	117	96	105	—	89		

quite a range of topography, on slopes from $0^{\circ}30'$ to 20° (average 8°). The soils have in common a rather thin crumbly topsoil, 7–15 cm deep, which is underlain by massive structured sandy loam or sandy clay loam. Deeper layers are greyish-brown or yellow-brown clays in the case of texture-contrast soil, or brown, reddish-brown, or yellowish-red sandy loams to sandy clays in the case of regosol, often with manganese concretions. The pH of the top layer varies between 5.5 and 8.5, of deeper layers between 4.0 and 8.0. About 30% of the ground is covered by litter, but the area covered by grit and gravel is much the same as in the *Themeda-Heteropogon* group.

The *Themeda-Sebima* group occupies the higher parts of the transects; it occurs on regosol on hills with slopes varying between 11° and 24° (average 15°). Only a 5–15 cm-deep sandy loam topsoil has a crumbly structure; deeper layers are sandy loams or finer textured soils, to clays, with a massive structure, dark brown, merging into reddish colours. Pieces of weathering rock are present, sometimes already at depths of 35 cm. The pH of the topsoil is 6.5–7.5, of deeper layers 5.0–7.0. About 38% of the ground is covered by litter and 25% by grit and gravel, whilst stones and rock fragments cover 3.5%.

The *Themeda* series occurs on the texture-contrast soil of transect 1. One of the main characteristics of its locality is the excessive cover of grit, which averages 53%. The *Themeda-Sorghum* series occurs on black clay soil, of which the upper horizon appeared to contain red soil material, which disturbance is presumably caused by wartime road works. The *Sebima-Heteropogon* series occurs on the steep hill slope of transect 2 (28°), which for almost half the surface is covered by rock outcrops and fragments.

With regard to an explanation for the rather simple group distribution pattern, there is no direct correlation with soil type or with slope angle. Differences in cover of grit and of stones, in the thickness of the crumbly topsoil, in the colour of the deeper soil layers, and in the nature of concretions they contain, however, do not rule out the possibility of a great influence of soil moisture regime. On the other hand, this influence was not closely expressed by the root

distribution, which will be treated in the next section. An autecological study of the grass species rather than investigation of group patterns might perhaps contribute more to an explanation. Factors also to be taken into account are, for instance, the frequency and intensity of fires, the severity of runoff, the lengths of periods of waterlogging, and ability for germination and regeneration. Observations at Katherine, N.T., Australia, have revealed a marked response of sward composition to short-term variations in rainfall, *Themeda australis* becoming dominant in drier years (Norman, 1963). A similar interaction could be expected to occur in the area of investigation.

ROOT SYSTEMS OF GRASSES: The distribution of the grass roots in the sections of the pits was studied by spraying the walls with a fine jet hose.

The root systems of *Themeda australis*, *Heteropogon contortus*, *Sebima nervosum*, and *Sorghum nitidum* appeared to be of much the same structure. Roots spread in horizontal, vertical, and intermediate directions from the tussock base, forming a dense "corona" with a radius of 1 or 2 dm which becomes more open at greater distances.

In the black clay soil the crumbly topsoil, especially the fine crumbly upper part, is densely rooted; numbers of roots gradually diminish in the underlying heavy clay; usually roots are frequent at 0.9 m and a few are still present at 1.8 m. Roots sometimes seem to follow the planes along which the clay cracks on drying; in other cases they seem to penetrate at random.

In the texture-contrast soil, horizontal roots spread densely through the superficial layer, about 10 cm thick, of friable sandy loam or loamy sand, with a fair amount of oblique and vertical roots penetrating in the underlying massive layer, which is rather resistant to washing. Roots penetrating in the clayey subsoil at about 0.3 m depth are usually few, about 4 per dm^2 , sometimes more, which may be due to a less massive structure of the topsoil. Deepest roots are observed at 1 m. Several grass roots penetrated deeper horizons by following the vertical roots of the eucalypts, closely pressed against the bark.

In the red regosol, roots spread in all directions in the superficial, crumbly layer and in

the upper part of the massive layer of the sandy (clay) loam, regardless of whether or not the surface shows terracettes. The density of the "corona" around the base of the tussocks is less than that in texture-contrast soil. Rather many roots penetrate deeper, into the layer with weathered rock fragments. Deepest roots are observed at 1.3 m.

Consequently, rooting patterns except for being somewhat more diffuse in the regosols are not very different in various kinds of soil, and only a firm, massive, sandy loam layer as encountered in certain texture-contrast soil profiles seems to be unfavourable for deeper root development.

Ecological Significance of the Results

The investigation revealed that correlations between vegetation and soil conditions seem to have only a localised validity. For instance, the distribution pattern of *Eucalyptus alba* encountered on transect 2, viz. its restriction to texture-contrast soils, is not consistent with that on transect 1, where *E. alba* occurs over the whole transect. Also, a hypothesis based on observations at transect 1, that the boundary between the *Themeda-Capillipedium* and the *Themeda-Sehima* ground cover groups coincides with the boundary between texture-contrast soil and regosol, would appear untenable when applied to transect 2. On the other hand, black soils carry only the *Themeda-Heteropogon* group, which however also extends over other soils.

Some conditions find ready expression in the vegetation (e.g., steep, rocky slopes are covered with a *Sehima-Heteropogon* ground cover, and disturbed soils with a *Themeda-Sorghum* ground cover), but generally the determining factors remain unknown. The presence of an algal cover, great local variations in grass cover, and differences in certain soil characteristics mentioned in the discussion on the ground cover groups, suggest a great influence of soil moisture, whilst terracettes and local concentrations of grit and gravel point to slope wash as an important factor. On the other hand, differences in moisture regime were hardly, if at all, expressed by rooting patterns as the root systems of the grasses as well as those of *E. papuana* appeared to be similar for different

soils, whilst *E. alba* showed a considerable variation within one soil type.

Observations over a period of years, also during the wet season, and on a regional basis could lead to more conclusive results, but an investigation into the influences of burning will probably reveal fire to be the overriding factor of the environment.

COMPARISON WITH AUSTRALIAN VEGETATION

Savannahs comparable in physiognomy and to a certain extent also in floristic composition occur in the higher rainfall areas of tropical and subtropical Australia, but relevant literature is scarce and is concerned mainly with the characteristics of the ground cover for use as natural pasture.

At Katherine, N.T., Arndt and Norman (1959) studied a savannah vegetation of a richer floristic composition but which included most of the species encountered at Port Moresby. Predominant in the ground cover are *Sorghum plumosum*, *Themeda australis*, and *Chrysopogon fallax*. The dry matter yield for unburnt areas of a lightly grazed pasture was about 110 g/m² at the end of the dry season (October), and rose to about 290 g/m² at the end of the wet (April–May). For areas burnt at the end of the dry season the dry matter yield at the end of the wet season was only about 140 g/m².

Shaw and Bisset (1955) have given figures for subtropical Queensland, which can be as low as 60 g/m² for dry season yield and as high as 425 g/m² for yields at the end of the wet season.

The figures obtained for the *Themeda australis-Eucalyptus* savannah in Papua are much higher than those mentioned above. Oven-drying of the samples instead of air-drying would have resulted in figures about 10 to 15% lower, which gives a figure of, say, 530 g/m², which still is much higher than the figures for Katherine and Queensland. Because our observations are from only one season, it is impossible to say how near they are to the average. On the other hand calculations by Fitzpatrick (1965) about the periods of useful pasture growth demonstrate that the growing season at Jackson's

Airport could be nearly twice as long as at Katherine, viz. 41 weeks against 22: this would certainly contribute to the difference in production between these stations.

ACKNOWLEDGMENTS

Grateful acknowledgment is made of the interest which Mr. R. A. Perry and the other ecologists of the Division of Land Research and Regional Survey have taken in this investigation, and also their criticism on the subsequent paper.

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Appreciation is expressed to the head of the Quarantine Station of the Department of Agriculture, Stock and Fisheries, Port Moresby, for putting a balance at my disposal and to the Director of the Department of Forests, Port Moresby, for lending wartime aerial photographs.

Last, but not least, I would like to thank Habau and Mou for their assistance in the field.

SUMMARY

Themeda australis-*Eucalyptus* savannah covers extensive areas in the monsoonal coastal lowlands of Papua. The ground layer is dominated by grasses, mainly *Themeda australis*, *Heteropogon contortus*, and *Sehima nervosum*; the tree layer is formed by three species of *Eucalyptus*.

This type of savannah has been investigated

on two transects near Port Moresby. Observations have been made on its composition and structure, and on rooting habits of trees and grasses. Quantitative data for the grass cover have been determined.

Patterns in the vegetation coincide only locally with some topographic and soil factors, and it is suggested that further investigation may reveal burning as an agent overriding the influences of other factors.

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A Stem Gall on *Muehlenbeckia australis* (Forst. f.) Caused by the Moth *Morova subfasciata* Walk.

B. C. ARNOLD¹

THE RAMPANT, much-branched liane *Muehlenbeckia australis* is a familiar sight in many New Zealand forests, reaching into the tops of trees 30 feet high with woody ropelike stems, or heaped in a tangled mass where no support is provided by other plants.

Among the branches of *Muehlenbeckia australis* are sometimes found persistent woody hypertrophies which arise as spindle-shaped or nut-shaped galls on one-year-old stems. The diameter of the young galls may be about five times that of the stems on which they arise (Fig. 1).

During the first year of growth, galls of *M. australis* are found to contain either the dark pupa of a moth, or the pale larva (Fig. 2) which actively feeds on the tissues of the pith. An exit passage for the later escape of the adult moth runs from the centre of the gall towards the surface, but stops short, separated from the outside wall by a thin membrane.

Galls from which the small tawny moths (Fig. 3) have emerged can be recognized by the open escape hole.

In a discussion on gall insects, Brues (1946) made a comparison of plant galls with animal tumours, stating that "the gall continues to develop only under the sustained action of the stimulating agent, while the growth of the animal neoplasm is not thus limited." Brues did not refer to the well known exception of crown gall (Mani, 1964), probably because of its relation to bacteria and not to insects. Brues' claim may be valid in a general way since few cases of the continued growth of galls in the absence of the causal agent have been reported. Undoubtedly the moth-induced gall of *M. australis* is one of the few known exceptions.

One aim of this study was to examine the histological make-up of the galls for any evi-

dence of cellular transformation which might be associated with differences in growth between the gall and the normal stem. A second objective was to test extracts of the moth larvae for growth-stimulating capacity on stems of seedlings of *M. australis*. Finally, it was hoped to induce galls under laboratory conditions with young living larvae, preferably newly hatched from eggs.

This work was supported by a research grant awarded by the University of Canterbury Grants Committee.

METHODS AND MATERIALS

Four dozen seedlings about 6 inches in length were dug up in the forest and grown separately in 4-inch plastic pots in a glasshouse in a mixture of gravel, sand, and garden loam. Growth over 18 months was active and healthy.

Five active larvae were removed from their galls and immersed entirely in 1 ml pure 100% acetone. The larvae were crushed thoroughly in the acetone in a glass vial with a glass rod and were left in the stoppered vial for a week. The acetone was evaporated with the temperature at 25°C. To the dry residue of the ground-up larvae in the original vial was added 2 ml anhydrous lanolin, which was mixed thoroughly with the larval material (using a glass rod) to give even dispersal.

To each of 12 *Muehlenbeckia* seedlings a small globule of the paste mixture was added in the axil of a young leaf near the stem tip.

With 12 other *Muehlenbeckia* seedlings, the tip of a shoot was removed in front of a node and a small blob of the paste mixture was placed on the cut surface on each plant.

On 12 other seedlings small blobs of paste mixture were applied to the abaxial surface in the centre of young leaves.

The remaining 12 seedlings were treated on cut shoot surfaces with plain lanolin lacking larval extract.

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Cuttings of stems bearing galls with larvae were obtained with about 20% success by placing the specimens in jars of clean tap water which was changed two or three times a week. Roots appeared within 14 days at room temperature.

Moths were raised under large bell jars in which gall-bearing twigs were enclosed, with the basal end of the twig in wet sand.

On the first occasion in March a female and a male moth hatched within 24 hours of each other. They were placed overnight in a separate bell jar containing fresh *Muehlenbeckia* shoots set in moist sand. In the morning some 30 orange-coloured eggs were found, laid in short rows, some on the glass walls of the bell jar and some on the *Muehlenbeckia* stems. Both moths were dead by the following day. Only one other moth hatched from the galls on this occasion, and that was a solitary female which emerged a few days later.

On a second occasion, in December, a male and a female moth emerged about the same time under bell jars in the laboratory. They were placed overnight in a covered beaker with a fresh leaf of *Muehlenbeckia*. Again eggs were laid, all of them on the walls of the beaker, but they were almost white, lacking the colour of those laid in March.

No eggs hatched, either of the white or the orange batch.

An attempt to induce galls artificially was made by removing three small active larvae from galls and placing them on separate plump softwood cuttings of young *M. australis* shoots. The shoots were kept in large covered glass jars with the cut ends immersed in small flasks of fresh tap water. Overnight the larvae burrowed into the stems, entering near the axil of the first prominent leaf. After 24 hours the entry holes eaten by the larvae had been closed by a smooth dark membrane. Within a week the shoots with the larvae inside had blackened and were beginning to die. Control shoots lacking the larvae also died a few days later.

Material of galls and normal stems for histological examination was fixed in Formo-acetic-alcohol, embedded in paraffin, sectioned serially at 10 μ and stained in safranin and fast green (Johansen, 1940).

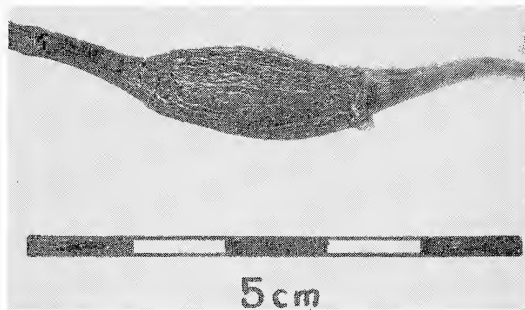


FIG. 1. A gall still occupied by the larval moth.

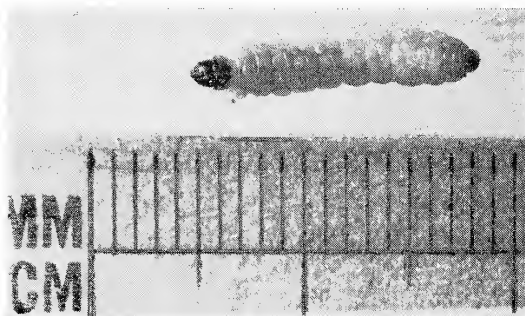


FIG. 2. Larva of *Morova subfasciata*.

OBSERVATIONS

Male adult moths were smaller, darker, and more active than females (Fig. 3). Neither survived more than a day after the eggs were laid.

The dates of emergence of the moths from galls were in agreement with Hudson's report (1928) that the perfect insect is to be found from December to March. Entomological details of the dark brown insect pupa and the pale larva (Fig. 2) are included in Hudson's descriptions and are not necessary here.

Since the eggs laid in the laboratory did not hatch, it was decided to use larvae from existing galls to attempt to induce new galls artificially. The results of allowing larvae removed from galls to penetrate cuttings of *Muehlenbeckia* shoots were inconclusive because the cuttings did not live long enough for galls to form. (The control cuttings also survived only a short time.)

However, it was seen that the larvae retained the ability to eat instinctively into the pith and to seal the entry hole. (When similar experiments were carried out by the author with larvae

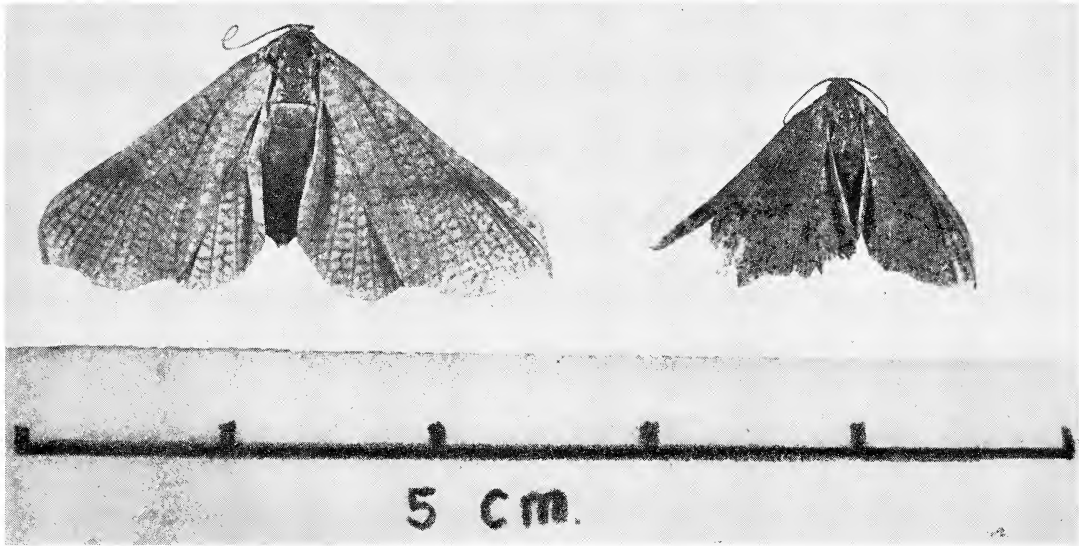


FIG. 3. Adult moths, female on the *left*.

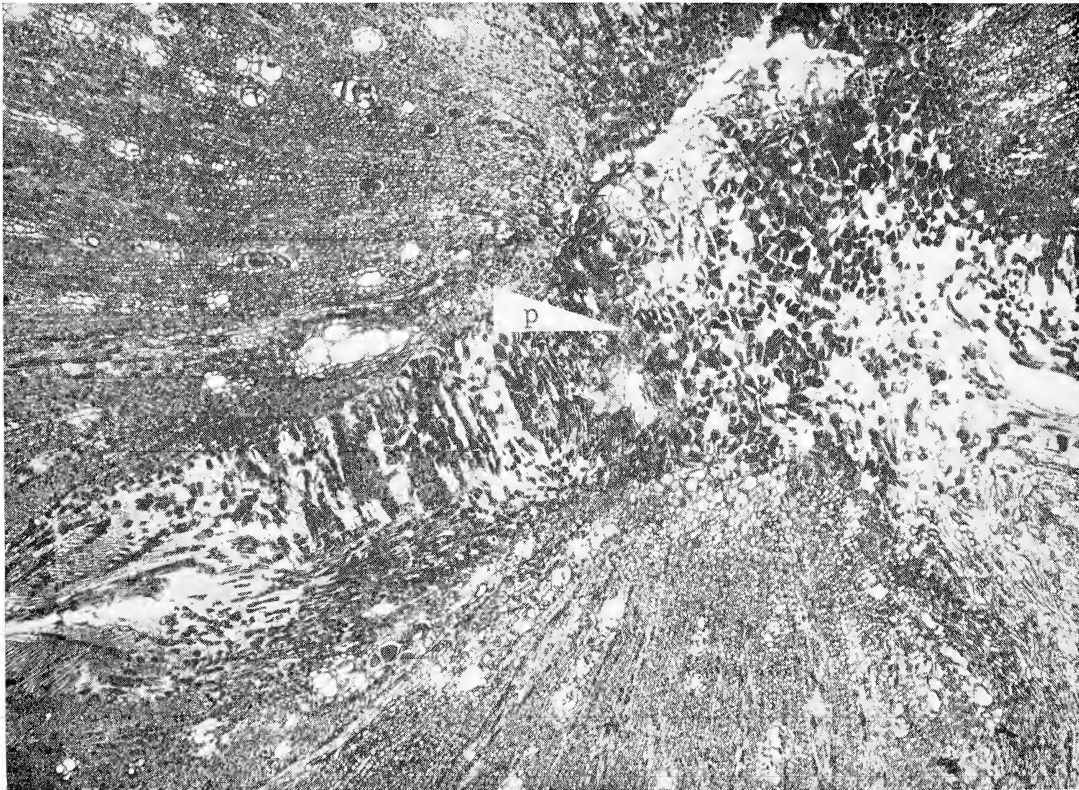


FIG. 4. Transverse section of gall showing invasive pith cells (*p*, pith cells).

of a species of gall midge, they failed to re-enter new shoots of the host plant.) With the larvae of *Morova subfasciata*, however, further work with intact seedlings, rather than cuttings, of *M. australis* might give promising results under laboratory or glasshouse conditions.

Such experiments depending on the feeding action of the larvae may be more fruitful than attempts to induce galls with larval extracts. In the experiments in which crude acetone extracts of larvae were applied to seedlings of *M. australis*, there was no sign of growth stimulation in the treated plants after 18 months, at which time the 48 seedlings were discarded.

Sustenance for the larva is provided by the continued growth of the pith cells of the gall. When living galls are cut open and kept moist in a petri dish, after removal of the larva, white callus-like proliferations of the pith become apparent to the naked eye after a week at room temperature. (If the larva is left inside a gall from which only a "window" of tissue has been removed, the larva forms a smooth dark membrane resealing the cavity in a few hours.) No callus-like proliferations are obtained from living galls from which the moth has departed; and it appears that the larva eventually consumes the entire pith tissue within the length of the gall.

A comparison of the anatomy of the gall with that of normal stems of *M. australis* shows some interesting differences which seem to account for the process of gall enlargement.

Serial cross sections through young galls and the adjacent portions of the stem show that the presence of the larva is associated with excessive growth of vascular rays and pith. The pith and vascular rays enlarge and actively invade the woody cylinder (Fig. 4), pushing outward to the cortex. At the same time, or shortly afterwards, the cambium itself becomes overactive, giving rise to further ray tissue of irregular starch-packed parenchyma. The end result of this excessive growth of pith, rays, and cambium is that the vascular cylinder is cleft into several cable-like strands (Fig. 5) which traverse the body of the gall like a cage around the larva.

In older normal stems of *M. australis* the

vascular cylinder resembles a scalloped column. Presumably this is the result of the cambium forming larger proportions of xylem than of phloem at the semicircular xylem lobes, and a corresponding excess of phloem in the V-shaped grooves between the lobes (Eames and McDaniels, 1925). This atypical growth of the cambium is associated with the laying down of conspicuous rays which are continuous in spoke-like fashion (in cross section) from the pith to the grooves between the xylem lobes.

Nevertheless, the normal stem of *M. australis* is a compact unity and not a composite of separated strands like the body of the gall or the typical stems of other lianes. It is well known that in several lianes anomalous activity of the cambium may give rise to a separation of the vascular system into ropelike strands (Eames and McDaniels, 1925).

Thus, the morphogenetic influence of the moth has been to initiate abnormally high growth rates and new growth patterns in the pith, rays, and cambium; and to produce the counterpart of advanced liane-type anatomy in a plant which by itself has not evolved far in this direction.

DISCUSSION

The tendency of the cambium of the normal stem of *M. australis* to produce conspicuous vascular rays and varying proportions of xylem and phloem at different sites could be taken as the suggestion of an evolutionary trend toward the type of stem structure seen in lianes with a vascular system composed of separated strands. Without this slight tendency being already inherent in *M. australis*, it is doubtful whether the larva of the gall moth would elicit such a dramatic anatomical transformation.

The persistence of the galls as an overgrowth after the departure of the insect may reflect merely the continued growth of tissues after a preliminary boost and reorientation, without indicating a truly tumorous condition, and may not be entirely contradictory to the concept of tumour growth implied in the statement of Brues (1946) quoted earlier. The initial invasiveness of pith and ray cells may reflect the stimulatory effect of wound hormones resulting

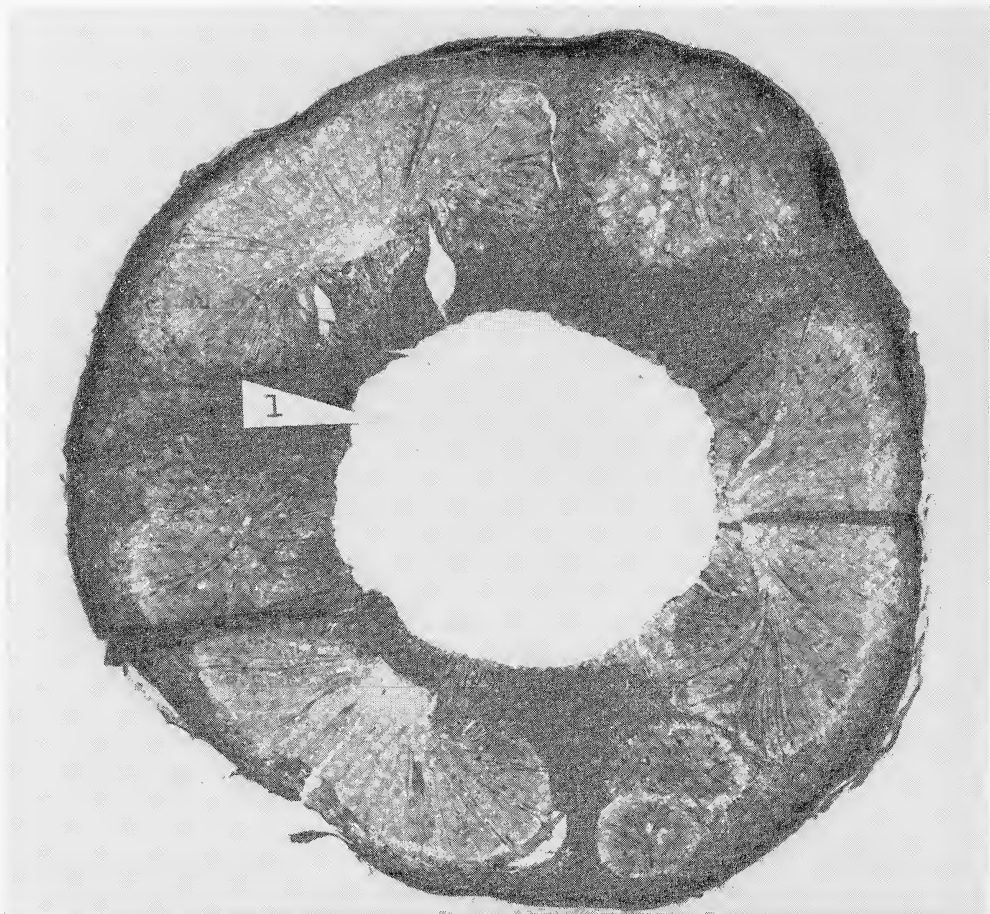


FIG. 5. Transverse section through gall showing division of vascular system into separate parts (1, larval cavity).

from the feeding action of the larva (Bloch, 1952) and may not represent a permanent cellular transformation such as appears to be the case in crown gall and in animal cancers. Electron microscope studies might prove illuminating in answering such questions, and should at least reveal the presence of any viruses or bacteria which might be associated with the larvae and which have not at present been detected.

Whatever adverse effects the larva and gall may have on *M. australis*, there is no obvious sign that translocation or transpiration is seriously impeded. This is probably because the ropelike divisions of the stele which run separately through the gall are united at either end and do not disrupt the continuity of the climbing stems which may extend to great heights.

SUMMARY

Stem galls on the liane *Muehlenbeckia australis* (Forst.f.) are caused by the larval form of the moth *Morova subfasciata* Walk., which feeds on proliferating tissue of the pith.

After the departure of the insect, the gall continues to grow without blocking translocation or transpiration in the stem.

Gall formation is brought about by excessive growth of the pith, vascular rays, and cambium, which separate the vascular cylinder into several ropelike portions which remain united at either end of the gall.

Applications of crude acetone extracts of young larvae failed to produce galls on seedlings of *M. australis* grown in a glasshouse.

Larvae removed from galls are capable of re-entering new stems and re-establishing themselves in the pith after sealing off the entry hole.

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Laboratory Formation and Characterization of Taranakite in a Hydrol Humic Latosol Soil from Hawaii¹

PO-LING LIU, G. D. SHERMAN, and L. D. SWINDALE²

ABSTRACT: The mineral taranakite was obtained in reactions between samples of an Akaka soil and monopotassium phosphate solutions ranging from 0.2 to 0.6 molar, at pH values of the reacting system ranging from 2.3 to 2.9. Characteristics of the reaction products were compared with those of pure synthetic taranakite, using X-ray, chemical, optical, infrared absorption, and differential thermal techniques.

The taranakite was essentially a potassium-aluminum-phosphate complex. There was no indication of isomorphous substitution of iron for aluminum. The molar ratios of K/PO_4 and Al/PO_4 of the reaction product were found to be 0.37 and 0.72 respectively. The taranakite was thought to be formed by precipitation of a soluble phospho-alumino complex anion together with potassium ions.

The possibility is suggested of the formation of taranakite when soluble potassium and phosphate react with Hydrol Humic and Humic Latosols in the field. During the early stages of reaction, the reaction product is believed to be cryptocrystalline, but the size of crystals increases with time.

IN HAWAIIAN SOILS large amounts of added phosphate often are rendered at least temporarily unavailable to plants. Davis (1935) attributed this phenomenon to an absorption effect in the soils. He found that, for any given equilibrium phosphate concentration, the amount of phosphate fixed varies directly with the ratio of soil to solution. Chu and Sherman (1952) reported that, in the presence of hydrated iron and aluminum oxides, as much as 90% of added soluble phosphate was fixed by the soils in a relatively short period of time. When the oxides were removed, less than 30% of the applied phosphorus was fixed. The Hy-

drol Humic Latosols showed the highest phosphorus-fixing capacities, but the Low Humic Latosols and Humic Latosols also fixed phosphorus to a considerable extent.

The manner in which phosphate is fixed in acid soils is as yet unknown, but in some instances it is likely to be in the nature of a solution-precipitation. Kittrick and Jackson (1955) reported, from electron microscope observations, that a solution-precipitation mechanism was operative in the reaction of phosphate with colloidal iron oxide particles and thin aluminum hydroxide films at room temperature. These authors also reported (1956) that there is a solution-precipitation mechanism operative in the reaction of phosphate with kaolinite and greenalite at room temperature. The reaction product in the potassium phosphate-kaolinite system was taranakite.

Several workers have identified phosphate complexes which could occur as reaction products in hydrous colloidal sesquioxide systems (Wada, 1959; Birrell, 1961; Lindsay et al., 1962; Tamimi et al., 1963; Tamimi, 1964). These phospho-reaction products have been associated with the presence of calcium, ammonium, and potassium cations in the system.

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Taranakite, or other similarly complex potassic alumino-phosphate minerals, appears to be the most likely reaction product to be identified in soils to which potash and phosphate fertilizers have been added together or over a short time interval. In this study a search was made for the presence of taranakite in a highly aluminous soil to which potash and phosphate fertilizers had been added.

Records of naturally occurring taranakite are rare. Bannister and Hutchinson (1947) studied several native taranakite minerals, and pointed out that taranakite is usually found under moist conditions in localities where phosphate solutions from bird or bat guano react with rock or clay. The formula is given as



Taranakite is massive, claylike, pulverulent to compact; its color is white-gray or yellowish-white, and it is very soft and unctuous to the touch. This mineral was first found in 1865 on rocks which were being used for bird colonies at Sugarloaves, Taranaki, New Zealand. The minerals minervite (France) and palmerite (Italy) have been found to be identical with taranakite. Chemical analysis of the taranakite occurring at Sugarloaves, Taranaki, New Zealand (Dana, 1951), is as follows (in %): K_2O , 4.20; CaO , 0.55; Al_2O_3 , 21.43; P_2O_5 , 35.05; H_2O , 33.06; Insol., 0.80; Cl , 0.46; SO_3 , trace; FeO , 4.45.

Murray and Dietrich (1956) also reported the occurrence of natural taranakite in a Virginia cave that was the home of a colony of bats. The taranakite was associated with brushite, a calcium phosphate mineral.

In artificial systems having soil constituents, crystalline phosphate products containing potassium and aluminum have been synthesized. Birrell (1961), in New Zealand, showed that the addition of monopotassium phosphate to allophane produces a taranakite, the X-ray diffraction pattern of which agreed well with the value given by Murray and Dietrich (1956). Lindsay et al. (1962) synthesized taranakite from Hartsells soil (from Tennessee) by adding monopotassium phosphate to the soil. Wada (1959) reported the identification of taranakite-like phosphate minerals resulting from the reaction of monoammonium phosphate

with allophane and halloysite. Lindsay et al. (1962) identified the reaction product of ammonium phosphate and Hartsells soil as ammonium taranakite. Tamimi et al. (1963) were able to identify an ammonium-taranakite by means of X-ray diffraction technique. The synthetic mineral was obtained from three Latosolic soils derived from volcanic ash—namely Akaka silty clay, Hilo silty clay loam, and Paauhau silty clay loam—by the addition of ammonium chloride or diammonium phosphate in the presence of phosphoric acid. The reaction products were similar to the taranakite-like minerals obtained by Wada from Japanese allophane and halloysite. Tamimi (1964) postulated that taranakite could form in soils having pH values ranging from 1.85 to 5.55, although no taranakite was identified in soils with a pH above 3.9. Haseman et al. (1950) also had indicated that synthetic taranakite is stable at pH values of about 1.7–5.3. Kittrick and Jackson (1956) found that taranakite can be formed at room temperature by the addition of molar potassium dihydrogen phosphate to kaolinite. Beaton et al. (1964) treated kaolinite with saturated, instead of one molar, monopotassium phosphate solution and found no evidence of taranakite formation.

In addition to chemical, optical, and X-ray methods, Arlidge et al. (1963) found that infrared spectroscopy and differential thermal analysis were valuable complementary methods to X-ray studies in the identification of taranakite and compounds of similar nature. Infrared spectroscopy, moreover, also gave information on their structure and degree of crystallinity.

MATERIALS

The sample selected for study was a subsoil of an Akaka silty clay loam taken from a steep road bank near the beginning of the forest reserve area on Kaiwika Road, approximately 5 miles west of the main Hilo-Hamaku Highway on the island of Hawaii. Sampling depth was from 12 to 30 inches. The sample had a pH value of 5.5 and was a smeary clay. The soil was dominated by amorphous hydrous oxides of aluminum and iron. It also contained small amounts of crystalline gibbsite, goethite, magnetite, mica, and quartz (Tamura et al., 1953).

The main amorphous mineral colloid is allophane-like, excepting that the silica-to-alumina ratio is too low for the value of allophane proposed by Ross and Kerr (1934). The mineral is amorphous to X-rays, and differential thermal analysis indicates only a single, low temperature endotherm at about 180°C. It resembles so-called stable allophane (Jackson, 1956) in that it is resistant to decomposition by dilute hydrochloric acid of pH 3.5 or 2% sodium carbonate solution. Characteristics of the allophane-like fraction of Akaka soil and other amorphous mineral colloids are shown in Table 1.

The Akaka soil is a member of the Hydrol Humic Latosol Group, and was described by Cline et al. (1955). Akaka soils have developed from volcanic ash, under a tropical rain forest with an average annual rainfall of more than 120 inches. They are highly hydrated in the natural state; the water content sometimes exceeds 300% of the oven-dry weight of soil. The Akaka soils have very low bulk densities ranging from 0.1 to 0.6. On dehydration they lose volume and exhibit an increase in particles of sand size; the dehydration is irreversible. An explanation of this irreversibility has been given by Sherman (1957); he reported that the pro-

cess of dehydration caused the crystallization of the hydrous oxides to gibbsite, to crystalline iron oxide minerals, or to alpha quartz.

Monopotassium phosphate was used in the experiments. It is a product (reagent grade) of General Chemical Division, Allied Chemical Corporation. The pH of the phosphate solutions was adjusted with hydrochloric acid.

Preparation of the Reaction Products for Characterization

The reaction products were prepared by the following procedure. A 5–15 g sample of wet Akaka soil was placed in a 200-ml pyrex beaker or pyrex glass container of suitable size, to which was added 100 ml of potassium phosphate solution ranging from 0.2 to 0.6 molar, with an initial pH value of 2. The glass container was wrapped in a plastic bag and kept at room temperature (about 25°–30°C). The contents were filtered after standing from 1 to 200 days, and the pH of the filtrate was measured. The pH of the filtrate serves more or less as an indication of the pH of the reacting system, which, in turn, predicts the possible species of ions that enter into reaction. The residue was washed with 60% methanol, 80% ethanol,

TABLE 1
CHARACTERISTICS OF THE ALLOPHANE-LIKE FRACTION OF AKAKA SOIL AS COMPARED
WITH OTHER AMORPHOUS MINERAL COLLOIDS* OF SOILS

TYPE OF AMORPHOUS MATERIAL	DIFFERENTIAL THERMAL INDICATION		SiO ₂ /Al ₂ O ₃	SOLUBILITY IN DILUTE ACID AND ALKALI
	Endotherms	Exotherms		
	°C	°C		
Allophane:				
unstable	150	960	0.3–2.0	high
stable	150	960	2.0	low
Silica	165–573	—	—	high
Alumina	110–500	—	—	high
Iron oxides	160	350–450	—	high
Titanium oxides	195	465	—	low
Allophane-like fraction of Akaka soil	180	—	0.8	low

* Jackson (1956:528).

and 95% ethanol by decantation (Wada, 1959) to remove excess phosphate. The finer fractions of the solid phase were collected on the filter paper. The coarser fractions were left in the glass container. Both fractions were then air-dried.

Potassium phosphate solutions having concentrations ranging from 0.2 molar to 0.05 molar, or from 0.6 molar to 1 molar, with initial pH values of 2–4, were also used, but crystalline reaction products did not form.

A taranakite sample was synthesized for comparison; the synthesis was made as follows: 20 ml of 65% phosphoric acid were mixed with an aluminum chloride solution containing 2.65 g of aluminum chloride. The mixture of phosphoric acid and aluminum chloride was filtered and diluted to 50 ml, and an aliquot was taken in a pyrex beaker and neutralized with 10% potassium hydroxide to a pH between 3.4 and 5.0. The beaker containing the flocculent precipitate was covered with a watch glass and kept in a 50°C water bath. The crystalline precipitate which formed was separated by filtration, washed with distilled water, and air-dried.

Characterization of Phospho-reaction Products by X-ray Analysis

The reaction products were identified by X-ray diffraction, using a Norelco X-ray diffractometer with copper K α radiation. The X-ray diffraction patterns obtained throughout this study were of powder samples.

The effect of heating on the crystalline substance resulting from the soil-phosphate system and on the synthesized taranakite was examined. Both were subjected to a range of temperatures from 60°C to 150°C. The products resulting from heat treatment were identified by X-ray diffraction.

X-ray diffraction patterns of the phospho-reaction products prepared by treating Akaka soil with solutions containing potassium phosphate, ranging from 0.2 to 0.6 molar at pH 2, showed these reaction products to be taranakite. D-spacings for taranakite and heated taranakite obtained in these experiments and by Haseman et al. (1950) are gathered in Table 2. The prominent peaks of natural taranakites from

Sugarloaves, Taranaki, New Zealand, and from Pig Hole Cave, Giles County, Virginia, are at 16.2, 7.6, 3.82 Å, and at 15.49, 7.82, 3.79 and 3.12 Å, respectively. The 16.2 and 15.49 Å peaks are the strongest. The synthesized taranakite produced in this experiment, and those of Haseman et al. (1950), showed the strongest peak at 15.7 Å; and strong peaks at 7.89, 3.81, 3.14 and at 7.35, 3.79, 3.13 Å, respectively. Except for the 7.89 Å peak given by the phospho-reaction product obtained from Akaka soil, the prominent peaks of natural and synthesized taranakite are similar to the reaction products obtained from the Akaka soil. Birrell (1961) identified a taranakite by treating a Tirau ash-clay fraction from New Zealand with potassium phosphate solution. The X-ray diffraction pattern of the taranakite studied by Birrell showed prominent peaks at 15.60, 3.81, and 3.13 Å, and is very similar to that of the phospho-reaction products obtained from the Akaka soil.

The reaction products resulting from soil-phosphate systems, and the synthesized taranakite, were heated to different temperatures in order to examine the dehydration products, as well as the effect of heating on crystallinity. The dehydration products resulting from the soil-phosphate systems and the synthesized taranakite were similar with d-spacings of 13.6, 6.8, 5.5, and 3.4 Å. This substance is a compound like Product B as synthesized by Haseman et al. (1950). Both the reaction product resulting from soil-phosphate systems and the synthesized taranakite became amorphous above 130°C.

Characterization of Phospho-Reaction Products by Chemical Analysis

The evaluation of K/PO $_4$ and Al/PO $_4$ ratios for the reaction product was difficult because of contamination of the reaction product by soil particles. Therefore, a factorial experimental design (Snedecor, 1956) with four replications at three levels of soil was prepared, using 5, 10, and 15 g samples of wet soil with a 0.4 molar potassium phosphate solution at pH 2. Phosphate was estimated by chlorostannous-reduced molybdophosphoric blue color in a hydrochloric acid system, following fusion of the sample with sodium carbonate, and decom-

TABLE 2
POWDER X-RAY DIFFRACTION PATTERNS OF THE HEAT-TREATED REACTION PRODUCTS, SYNTHESIZED TARANAKITE
AND PRODUCT B OF HASEMAN ET AL. (1950)

PHOSPHO-REACTION PRODUCTS PRODUCED FROM AKAKA SOIL, DAYS OF STANDING													
5		54				200							
70 C		120 C		90 C		105 C		90 C		100 C		110 C	
d	Ch. I*	d	Ch. I	d	Ch. I	d	Ch. I	d	Ch. I	d	Ch. I	d	Ch. I
7.43		15.7	↓	13.6	↓	13.6	↓	13.6	↓	13.6	↓	13.6	↓
5.53	↓	13.6		7.37		7.43		7.43		7.43		7.43	
4.29	↓	7.37		6.86		7.08		7.08		7.08		7.08	
3.40		5.55		5.55		6.86		6.86		6.86		6.86	
3.33		4.29	↑	4.33	↑	5.57	↑	5.57	↑	5.57	↑	5.57	↑
3.03	↑	4.15		4.15		4.35		4.35		4.31		4.31	
2.81	↓	3.40	↓	3.66	↓	4.31	↓	4.31	↓	4.15	↓	4.15	↓
		3.15		3.61		4.15		4.15		3.67		3.67	
		2.91		3.40		3.69		3.69		3.54		3.54	
		2.81	↓	3.15	↓	3.40	↓	3.40	↓	3.40	↓	3.40	↓
				3.02		3.16		3.16		3.16		3.16	
				2.90		2.91		2.91		3.03		3.03	
				2.77		2.81		2.81		2.91		2.91	
						2.80		2.80		2.77		2.77	
						2.77		2.77		2.69		2.69	
										2.66		2.66	

* Change in intensity: ↑ represents increase in intensity.
↓ represents decrease in intensity.
Note: Prominent peaks of dehydrated taranakite are underlined.

TABLE 2 (Continued)

SYNTHESIZED TARANAKITE												PRODUCT B OF HASEMAN ET AL.				
70 C			80 C			90 C			100 C			130 C			d	I/I**
d	Ch. I*		d	Ch. I		d	Ch. I		d	I		d	Ch. I			
15.7	↓		15.7	↓		15.7	↓		13.6	S		13.6	↓		13.8	1.00
7.89	↓		13.8			13.6	↑		7.37	M		7.37	↓		7.35	.68
7.43			7.89	↓		7.43	↑		6.80	M		6.80	↑		6.79	.51
5.86	↓		7.43	↑		5.53	↑		5.53	M		5.53			6.05	.15
4.31			5.81	↓		4.29	↑		4.29	M		4.29	↓		5.46	.68
4.14			5.57			4.13	↑		4.13	M		4.13	↓		4.26	.40
3.80	↓		4.31			3.57			3.66	W		3.66	↓		4.14	.51
3.73			4.13	↑		3.40	↑		3.53	W		3.40	↓		3.89	.04
3.72			3.80	↓		3.13	↓		3.40	S		3.14	↓		3.64	.24
3.57	↓		3.73	↓		2.91	↑		3.14	M		3.03	↓		3.50	.16
3.40			3.72	↓		2.84			3.03	M		2.91			3.39	1.00
3.35	↓		3.57	↓		2.81			2.91	M		2.81	↓		3.13	.49
3.29	↓		3.40	↑					2.81	M		2.77	↓		3.01	.40
3.13	↓		3.13						2.77	M					2.90	.64
2.84			2.91												2.84	.11
2.81	↓		2.84												2.79	.38
2.73	↓		2.81	↓											2.76	.40
2.62	↓														2.74	.25
															2.68	.16
															2.64	.24
															2.56	.09

* Change in intensity.
** Visual estimates of peak intensities.
Note: Prominent peaks of dehydrated taranakite are underlined.

position of the melt with hydrochloric acid (Jackson, 1958). Potassium was determined by the flame photometer method, using a Model 21 Coleman Flame Photometer. Aluminum was analyzed by Chenery's colorimetric method, as modified by Moomaw et al. (1959). The entire experiment was repeated 10 times. A homogeneity test was conducted using the M-value as the criterion (Hartley, 1944). In its final form, the M-test involves computing

$$M = (n_1 + n_k) \log_e \frac{n_1 s_1^2 + \cdots + n_k s_k^2}{n_1 + \cdots + n_k} - (n_1 \log_e s_1^2 - n_k \log_e s_k^2)$$

where there are k samples, n_1, \dots, n_k , are the respective degrees of freedom and s_1^2, \dots, s_k^2 the respective estimates of variance. The homogeneity test showed that 3 of the 10 experiments were not homogeneous with the others and therefore they were rejected. Data obtained from the 7 remaining experiments were combined. Analysis of variance with respect to the ratios K/PO_4 and Al/PO_4 were carried out. The amounts of soil used did not affect significantly the ratios K/PO_4 or Al/PO_4 .

The possibility of isomorphous substitution of iron for aluminum in the reaction product, under the conditions of investigation, was also examined. Relatively pure crystalline reaction products were selected and were ignited over a Meker Burner. When ignited, the crystals should show a reddish color if iron-substituted taranakite is present. This did not occur; upon ignition, the iron-containing compounds gave hematite.

The average values of K/PO_4 and Al/PO_4 obtained from the seven experiments were considered to be taken from a representative sample because the M-test proved to be nonsignificant. The molar ratios of K/PO_4 and Al/PO_4 for the reaction products were 0.37 and 0.72, respectively. Those for the synthesized taranakite were 0.37 for K/PO_4 and 0.60 for Al/PO_4 . These values are very close to the ones calculated from the formula of taranakite established by Smith and Brown (1959), which is 0.38 for K/PO_4 and 0.63 for Al/PO_4 . The molar ratio Al/PO_4 for the reaction products is somewhat higher because the reaction prod-

ucts from the soil-phosphate systems were contaminated with Al-containing soil particles.

From the preceding experiments it is clear that the active constituent reacting with phosphate in Akaka soil is aluminum rather than iron. Recent work on the precipitation of phosphate in acid soils by Taylor et al. (1964) also revealed that aluminum hydroxide is the principal reagent in the precipitation of phosphate from fertilizers in acid soils.

Characterization of Phospho-reaction Products by Optical Methods, Infrared Analysis, and Differential Thermal Analysis

Optical properties of the reaction products from the soil-phosphate systems and from synthesized taranakite were determined. In addition to the synthesized taranakite already described, a second synthetic preparation was prepared as follows: 10 ml. of 1.5 molar monopotassium phosphate solution was mixed with a solution containing 0.25 g aluminum by vigorous stirring. The pH of this mixture was adjusted to 4.0 with 10% potassium hydroxide. The precipitates formed were kept in water at 50°C for a period of time. They were then filtered, washed with distilled water, and air-dried.

Immersion liquids were used to determine refractive indices. Other optical properties were studied by using thin sections of minerals mounted in Lakeside 70 Transparent Cement.

When examined under the polarizing microscope, both the reaction products obtained from the soil-phosphate systems and the synthesized taranakite were biaxial negative with a very small value of 2V. The refractive indices determined for the phospho-reaction product were $n_\alpha = 1.504$, $n_\beta = 1.507$, $n_\gamma = 1.509$, and $n_\gamma - n_\alpha = 0.005$. Those for the synthesized taranakite were: $n_\alpha = 1.503$, $n_\beta = 1.505$ and $n_\gamma = 1.506$, $n_\gamma - n_\alpha = 0.003$. These values are in reasonable agreement with those obtained by Haseman et al. (1950). The crystals are colorless and occur as tiny columnar aggregates. The aggregates of crystals tend to grow together, perpendicular to each other in pairs, to form a twinlike crystal in a rosette pattern, displaying a pseudo-hexagonal outline.

Smith and Brown (1959) re-examined the

synthesized taranakite prepared by Haseman et al. (1950) and considered that the taranakite was hexagonal and uniaxial negative. In the original report Haseman et al. described their synthesized product as pseudo-hexagonal and biaxial negative. It seems that taranakite might exist dimorphously, with $2V$ values ranging from 0 to about 20 degrees.

Infrared analyses of the phospho-reaction product and the synthesized taranakite were carried out. The phospho-reaction product from the Akaka soil was formed with 0.4 molar potassium phosphate, at pH 2, and 5 g of wet soil. The reacting system was left to stand for 200 days before the reaction product was collected. Purification of the phospho-reaction products was conducted by repeated reprecipitation with potassium hydroxide in phosphoric acid solution. The samples were ground, mixed with potassium bromide, and pressed into discs, and infrared spectra were obtained using a Beckman infrared spectrophotometer.

The infrared spectra of the phospho-reaction product produced from Akaka soil, and of the synthesized taranakite, in pressed KBr discs, were in good correspondence with each other. The patterns obtained are shown in Figure 1. Absorption peaks near 3400 cm^{-1} showed the presence of water of crystallization. Corbridge and Lowe (1954) reported that all hydrated salts absorb in the 3300-cm^{-1} and 1640-cm^{-1} regions, which presumably correspond to O-H stretching and O-H bending, respectively. Complex phosphate absorption bands between 1200 cm^{-1} and 870 cm^{-1} and P-OH linkages near 2500 cm^{-1} indicated the presence of PO_4^{3-} and acidic phosphate ions, respectively (Corbridge, 1956). These values are very close to the infrared absorption spectrum for taranakite obtained by Arlidge et al. (1963).

Differential thermograms of the phospho-reaction product and the synthesized taranakite samples were obtained. The differential thermal setup is the same as the one described by Uehara and Sherman (1956).

The differential thermal curves show that both the phospho-reaction product produced from the Akaka soil and the synthesized taranakite undergo endothermic reactions at about 230°C and exothermic reactions between 500°

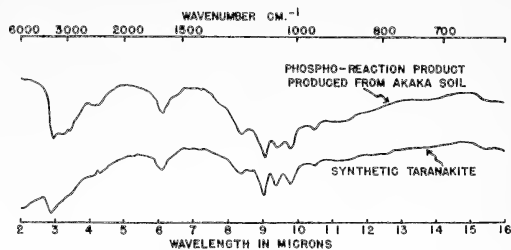


FIG. 1. Infrared absorption spectra of soil-phosphate reaction product and pure synthesized taranakite.

and 600°C . These differential thermal curves, which are shown in Figure 2, indicate that the phospho-reaction products from Akaka soil and the synthesized taranakite both lose their water of crystallization in one stage, as evidenced by the endotherm at 230°C . Arlidge et al. (1963) found similar peaks from samples supplied by the Tennessee Valley Authority, but natural taranakite from Pig Hole Cave and a synthetic taranakite lost their water of crystallization in two stages. This variation is thought to be associated with variations in degree of crystallinity of particle size. The exothermic peak between 500°C and 600°C probably represents the recrystallization of the mineral after it has been dehydrated, as suggested by Murray and Dietrich (1956). The differential thermal gravimetric curves for taranakite obtained by Arlidge et al. (1963) revealed that there is no weight change during the process of exothermic reaction, indicating the possibility of recrystallization.

The fact that all the taranakite samples studied in this experiment are amorphous to X-rays when they are heated above 130°C shows that the recrystallized products from dehydrated taranakite are too small or too poorly ordered to be identified by X-ray diffraction.

The Effect of Time on Crystallite Size of the Phospho-reaction Product Produced from the Akaka Soil

The relationship, $n\lambda = 2d\sin\theta$, deduced by Bragg, describes the conditions under which electromagnetic waves reflected from a set of planes in a crystal will be in phase with each other. The relationship requires that the planes be semi-infinite in the two dimensions perpen-

dicular to the normal about which the waves are reflected.

For crystals or particles below 20μ in diameter, this requirement is no longer fulfilled and deviations from the Bragg equation become apparent. As the crystals or particles get smaller, the deviations become larger; they are shown in X-ray diffraction patterns by an increasing broadening of the recorded reflections. Conversely, the breadth of the reflections can be used as a measure of particle size. The methods by which this may be done are described in any standard text on X-ray diffraction methods (see Henry, Lipson, and Wooster, 1951). The effect of time of crystallization on crystallite size may be studied by these methods. In this study 5-g portions of the wet Akaka soil were treated as follows: (a) With 0.4 molar potassium phosphate at pH 2. The reaction system was left to stand for 5, 54, and 200 days. The finer fraction of the solid phase was filtered, washed, and dried, as usual. The half-peak breadths of the 15.7 \AA peaks were measured and were plotted (log scale) against time. (b) With 0.5 molar potassium phosphate at pH 2 for 6, 10, and 15 days. The preparations were washed and dried as before. The half-peak breadths of the 15.7 \AA peaks were plotted (log scale) against time of preparation. The results are shown in Figure 3. The crystal size of the taranakite increases with time, in accordance with expectation.

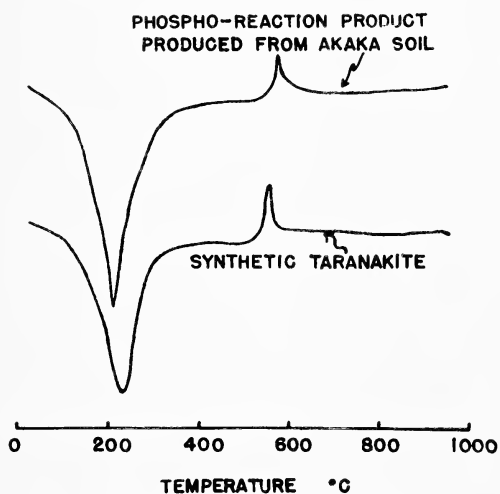


FIG. 2. D.T.A. curves of soil-phosphate reaction product and pure synthesized taranakite.

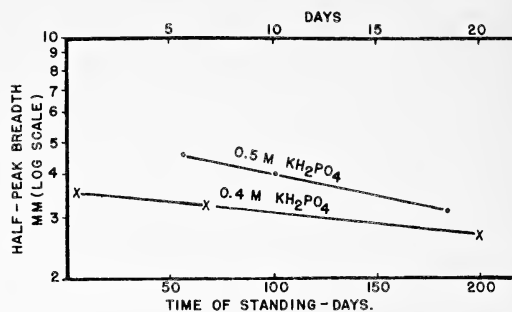


FIG. 3. Relationships between crystal size as measured by half-peak breadth and time of preparation.

DISCUSSION

Clearly identifiable taranakite was produced under the conditions of the experiments; that is, with weights of soil varying from 5 to 15 g, and with 0.2 to 0.6 molar solutions of potassium phosphate adjusted to pH 2. The pH values of the filtrate, and presumably of the reacting system, varied from pH 2.3 to 2.9. Many other concentrations of potassium phosphate and other pH values were tried, but nowhere outside and above that range was crystalline taranakite detected.

Chemical analysis gave K/PO_4 and Al/PO_4 ratios close to those obtained with synthetic samples, although the results for Al/PO_4 did show that some contamination of the crystals with soil material had occurred. The contamination did not cause significant differences to appear between infrared patterns or differential thermograms of soil-derived and synthetic taranakites.

The taranakite was probably formed by a series of reaction steps. The initial step would be the dissolution of Al^{3+} ions from the amorphous, hydrous oxides, followed by the formation of a complex anion by reaction between Al^{3+} and H_2PO_4^- , and finally by precipitation with K^+ ions. Although the Al^{3+} ions will be hydrated in solution, the infrared and differential thermal patterns indicate that water is not a structural constituent of the complex anion.

No crystalline taranakite was detected at the pH values which are common to Akaka soils in the field. However, from the evidence obtained here and from a review of the literature, it is reasonable to suppose that a cryptocrystalline

form of taranakite is formed when heavy applications of fertilizers containing potassium phosphate are made to soils of the Hydrol Humic and Humic Latosol groups. Current applications by sugar cane producers range as high as 175 lb of P and 600 lb of K per acre for each planting or ratoon crop. Because of the heavy rainfall the soils are continually wet. Concentrated solutions of potassium phosphate have a pH of 4, at which value Al^{3+} cations and H_2PO_4^- anions exist in solution. Many times during the decomposition of the applied fertilizer, the concentrations will rise high enough in the subsurface horizons of the soil to enable cryptocrystalline precipitates to form. With time these precipitates can be expected to grow into larger and better-ordered crystals of taranakite.

CONCLUSIONS

1. Crystalline taranakite formed when the Akaka soil was treated with potassium phosphate solutions ranging from 0.2 to 0.6 molar and the pH value of the reacting system ranged between 2.3 and 2.9. On heating, the phosphate reaction products and a synthesized taranakite gave similar dehydration products.

2. The taranakite was essentially a potassium-aluminum-phosphate complex. There was no indication of isomorphous substitution of iron for aluminum. The molar ratios of K/PO_4 and Al/PO_4 for the reaction product were estimated to be 0.37 and 0.72, respectively, which agreed well with values found for the synthetic mineral.

3. Optical analysis showed that the taranakite crystals were colorless and pseudo-hexagonal in form. They were biaxial negative. The refractive indices were $n_\alpha = 1.504$, $n_\beta = 1.507$ and $n_\gamma = 1.509$, respectively, $n_\alpha - n_\gamma = 0.005$.

4. Structural diagnosis by means of infrared spectroscopy of the potassium-aluminum-phosphate complex revealed that water of crystallization, $(\text{PO}_4)^{3-}$ ions, and P-OH linkages were all present.

5. Differential thermal data showed that both the phospho-reaction product and the synthesized taranakite underwent an endother-

mic reaction at about 230°C, and an exothermic reaction between 500°C and 600°C.

6. It is proposed that potassium and phosphate ions from heavy applications of fertilizer may react with aluminum ions in soil solutions in the subsoils of Hydrol Humic and Humic Latosols to produce cryptocrystalline precipitates which, with time, will grow and transform into crystalline taranakite.

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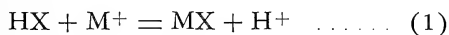
On the Exchange Properties of Allophanic Clays¹

K. H. HOUNG, G. UEHARA, and G. D. SHERMAN²

THE ORIGIN OF THE EXCHANGE SITES on the clay minerals has been considered to be due to isomorphous replacement of Mg for Al in the octahedral layer and/or Al for Si in the tetrahedral layer and to the broken bonds at the edges of the crystals. The charges originated by the former mechanism are supposed to be pH-independent and are called permanent charges, while the charges due to the broken bonds are considered pH-dependent (Coleman and Mehlich, 1957). A more detailed classification of charges on the clay surface has been proposed by Mehlich (1960). These negative charges can be compared with acid groups of cation-exchange resins; the permanent charges resemble the strong acid groups, and the pH-dependent charges resemble the weak acid groups. The pH-dependent charges show stronger affinity for the hydrogen ions, so that only when the metal ion activity of the external solution becomes much greater than that of hydrogen ion activity can they be saturated with the metal ions. It is evident that the activity ratio of metal ions and hydrogen ions is the main factor that determines the degree of saturation with respect to the metal ions.

THEORETICAL

If an ion exchange reaction takes place according to the following equation:



where X is the ion exchanger, an equilibrium equation is obtained:

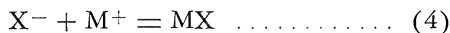
$$K = \frac{(MX)(H^+)}{(HX)(M^+)} \quad (2)$$

If (MX) and (HX) are expressed in terms of mole fractions of the cations occupying the exchange sites, it is reduced to Vanselow's exchange equation (1932), and K can be calculated from the measurable quantities.

If the exchange reaction is expressed as the sum of the following two reactions:



and



with Ka and Ks as their equilibrium constants:

$$K_a = (H^+)(X^-)/(HX) \quad (5)$$

$$K_s = (M^+)(X^-)/(MX) \quad (6)$$

then Equation (2) can be expressed as:

$$K = K_a/K_s = (MX)(H^+)/[(HX)(M^+)] \quad (7)$$

In equation (7), K is given as the ratio of two dissociation constants Ka and Ks. Assuming the exchange capacity is A, an expression of the degree of saturation of the exchanger with respect to M ions can be derived as follows:

$$(MX) + (HX) = A \quad (8)$$

$$\frac{K_a}{K_s} = \frac{(MX)(H^+)}{[A - (MX)](M^+)} \quad (9)$$

and, in rearranging the above equations, we have:

$$\frac{(MX)}{A} = \frac{1}{\frac{K_s(H^+)}{K_a(M^+)} + 1} \quad (10)$$

By arbitrarily setting values for Ks/Ka and (H⁺)/(M⁺) of the equilibrium solution, a family of curves is obtained, as shown in Figure 1. If the exchanger contains two different acid functional groups with Ks/Ka of 10⁴ and 10⁸,

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respectively, in equal amounts, a curve with two inflection points (such as is shown in Fig. 1A) is obtained. This fact provides a possibility of characterizing different functional groups that may be present on the clay surface, if the constants K_s/K_a differ by a factor of 10^4 or greater.

It is important to note that in a given exchange material the factors governing the degree of saturation by a specific cation are the ratio of the cation and the relative affinity of the exchanger toward the cations, as expressed by the ratio K_s/K_a . If the acid functional groups are very weakly dissociable, it is impossible to saturate the exchanger by repeated treatment of the exchanger with the electrolyte solution unless the metal ion concentration of the solution is extremely high and the hydrogen ion concentration is extremely low.

EXPERIMENTAL PROCEDURE

A 1-g sample of soil or 0.2 g of soil colloid was placed in the carbon funnel and plugged with balls of filter pulp to serve as the filtering medium. A series of samples thus prepared were leached with 1N NaOAc solutions previously adjusted with NaOH or HOAc to give various pH values covering the range 4.5–10. Increments of the leachates were collected from time to time for pH measurements. Leaching was continued until the pH of the leachate became identical with or close to the value of the original solution. The samples were then leached with 150 ml of methyl alcohol while maintaining a 2–5 mm head over the sample. After the alcohol washing, the samples were leached with 1N NH_4OAc in the same manner, and the leachates were collected in 50 ml volumetric flasks. The sodium concentration was determined by flame photometry, using a Beckman DU spectrophotometer.

Poor buffering of the sodium acetate solution at higher pH range made it necessary to use unusually large amounts of leaching solution before the pH of the leachate approached that of the solution. Similar buffering problems were encountered in the acid range by Schofield (1949) and Iimura (1961) when ammonium chloride was used.

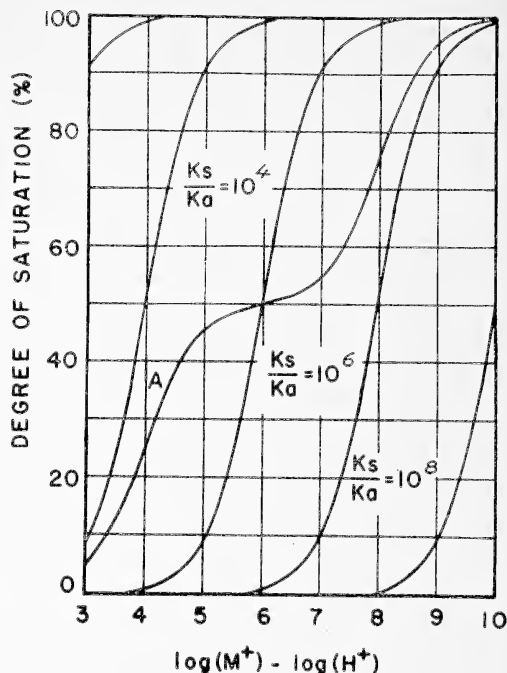


FIG. 1. Theoretical exchange curves. Curve A is the exchange curve of a hypothetical exchanger containing two kinds of acid functional groups in equal amounts, one with $K_s/K_a = 10^4$, the other with $K_s/K_a = 10^8$.

In the later part of this experiment, sodium carbonate solutions adjusted to the same pH value as that of the sodium acetate solutions were used prior to the leaching by sodium acetate solutions. Displacement of sodium carbonate solutions with sodium acetate solutions was necessary, since sodium carbonate is quite insoluble in alcohol.

MATERIALS

Silica gel. This sample, manufactured for chromatographic work, was obtained from the Baker Chemical Company. Particle size ranged from 0.18–0.07 mm. The appearance of a broad band near 3.7 Å on the X-ray diffraction pattern indicated that this material was essentially noncrystalline.

Halloysite. Sample mined in Eureka, Utah, and obtained through Ward's Natural Science Establishment, Inc.

Kaolin. Sample obtained through McKessen and Robbins, Inc.

Bentonite. Chiefly dioctahedral montmorillonite of uncertain origin, admixed with some quartz.

Soils. Samples of four soil profiles were collected from the slopes of Mauna Kea, island of Hawaii. All of these profiles have developed from volcanic ash, but their mineralogies vary considerably with changes in climate. One of the soils was of the Hanipoe series (Latosolic Brown Forest), two were of the Waimea series, hereafter referred to as Waikii and Mahoelua (Reddish Prairie), and the fourth was of the Waikalua series (Reddish Brown). The soils have been listed in decreasing order of weathering. The first three soils were composed chiefly of noncrystalline colloids; halloysite was the main clay mineral in the Waikalua series. These soils were treated with hydrogen peroxide to remove organic matter, washed with water, air-dried, and sieved through a 60-mesh screen. All soils used in this study have been described in the Soil Survey of the Territory of Hawaii, 1955.

Clay fractions. The $<1\mu$ fractions of these soils were separated, air-dried, and ground to pass a 100-mesh sieve.

Aluminum hydroxide A. Powder, obtained from Baker Chemical Company. X-ray diffraction pattern showed this to be pure gibbsite.

Aluminum hydroxide B. Precipitated from alkaline solution by carbon dioxide. Electrolytes were removed by prolonged dialysis and final removal was accomplished by electro dialysis. It was shown to be gibbsite.

Aluminum hydroxide C. Precipitated from alkaline solution by hydrochloric acid at a pH of about 7, washed with water and acetone, and air-dried. It was noncrystalline.

Aluminosilicate gels, A_1 and A_2 . Mixed solutions of sodium silicate and sodium aluminate neutralized by carbon dioxide. The precipitate was washed free of electrolytes in Buchner funnels.

Aluminosilicate gels, B_1 , B_2 , B_3 , and B_4 . Mixed solutions of sodium silicate and sodium aluminate acidified to a pH of about 7 with hydrochloric acid. After standing overnight, they were washed in Buchner funnels until free

of chloride ions. Acetone was used in the final washing.

RESULTS AND DISCUSSION

Clay Minerals and Allophanic Soils

The results obtained on clay minerals and allophanic soils are shown in Figures 2 and 4. All leaching solutions were 1N with respect to sodium ions, and it is fairly safe to take pH as the abscissa in lieu of $\log (M^+) - \log (H^+)$. Without knowledge of the cation-exchange capacities, the amounts of sodium ions held on the exchanger were plotted against the pH of the final leachates.

As shown in Figure 2, the bentonite adsorbed the same amount of sodium ions regardless of the pH of leaching solutions. In comparing this curve with the theoretical curves shown in

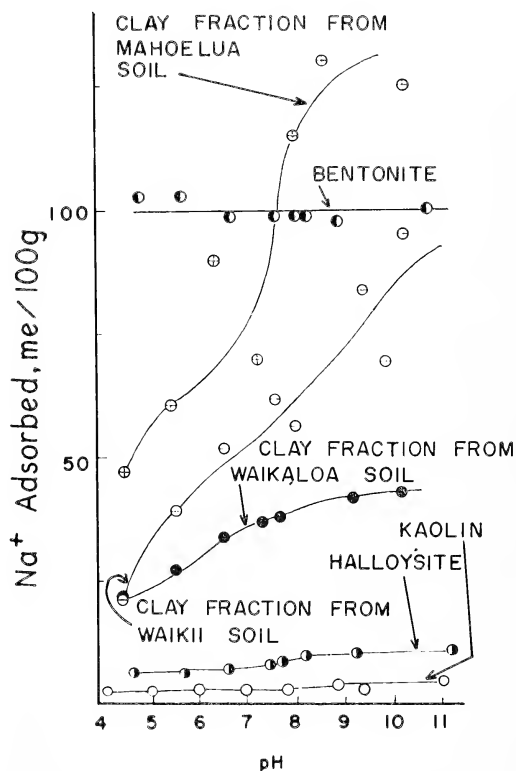


FIG. 2. Exchange curves of clay minerals and soil clays. ●, Bentonite; ○, kaolin; ◐, halloysite; ○, clay fraction from Waikii soil; ◐, clay fraction from Mahoelua soil, and ●, clay fraction from Waikalua soil.

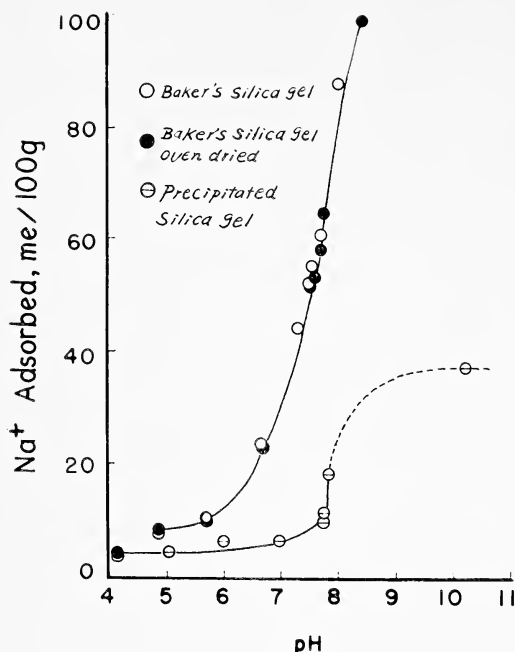


FIG. 3. Exchange curves of silica gels.

Figure 1, it is found that K_s/K_a for the acid functional groups of bentonite is about 10^2 or less. This implies that sodium ions are held on the montmorillonite clay with the same affinity as are the hydrogen ions. The amount of sodium ions adsorbed by halloysite and kaolinite is very small and partly pH-dependent. The inflection points near pH 8 indicate that the acid-functional groups of the pH-dependent part have a K_s/K_a value of about 10^8 . The hydrogen ions associated with these functional groups cannot be replaced by sodium ions unless the $(Na^+)/(H^+)$ ratio of the solution becomes greater than 10^{10} . This suggests covalent bond formation between the functional groups and the hydrogen ions; simple ionic interaction between the negative charges and the hydrogen ions seems to be inadequate to explain this phenomenon. A comparison of these curves with those of silica gels shown in Figure 3 indicates that these charges on kaolinite and halloysite most probably are due to the surface hydroxyls attached to silicon atoms.

Aluminum Hydroxides

Aluminum hydroxides A and B both failed to show cation exchange to an extent that could

be considered of real importance. The amount of sodium ions adsorbed under the pH range studied were always less than 1 me. per 100 g. Aluminum hydroxide C had a maximum exchange capacity of about 6 me. per 100 g, showing an inflection point near pH 8. The amount of sodium ions adsorbed at pH 4.5 was about 1 me. per 100 g.

Synthetic Aluminosilicate Gels

That the tetrahedrally coordinated aluminum atoms produce exchange sites was suggested by Iler (1955), and by De Kimpe, Gastuche and Brindley (1961). Such tetrahedrally coordinated aluminum atoms were postulated as the source of exchange capacity of soil allophanes by Iimura (1961). In this investigation, the aluminosilicate gels studied were prepared from alkaline solutions so as to arrange the aluminum atoms in the tetrahedrally coordinated positions, as much as possible. Their compositions, as well as the maximum cation exchange capacities, are listed in Table 1. Their exchange curves are shown in Figure 5.

It is striking that the CEC/Al ratios of the gels with silica-alumina ratios greater than 0.7 are very close to 1, indicating that each negative charge on the gel is associated with one aluminum atom. If the CEC of the gel is entirely attributed to the tetrahedrally coordinated aluminum atoms in gel A₂, it turns out that about 60% of the tetrahedral positions in the gel are occupied by the aluminum atoms. In gel A₁ the same calculation reveals that the tetrahedral positions occupied by the aluminum atoms would be as high as 62%, and that this amount may be the practical limit for the aluminum atoms to take the tetrahedral positions in the aluminosilicate gels under the specified conditions of preparation. Iler (1955), on the other hand, states that the maximum amount of aluminum atoms which can be tetrahedrally coordinated in the aluminosilicate gels is 50%.

The surface silanol groups of these synthetic gels apparently do not dissociate under the conditions of the experiment, and thus do not contribute to the CEC. The negative charges caused by these tetrahedrally coordinated aluminum atoms are relatively strong in acid character (that is, readily dissociable), and their

presence seems to suppress the dissociation of the surface silanol groups.

Comparison of Sodium Adsorption with Ammonium Adsorption

The same procedure was applied to the Hanipoe surface soil, using 1N NH_4Cl and 1N NH_4OAc solutions. Concentrated ammonia and hydrochloric acid solutions were used to adjust the pH values of NH_4Cl solutions; concentrated ammonia solution and glacial acetic acid were used to adjust the pH values of NH_4OAc solutions. The final total concentration of NH_4^+ ions was not 1N, but varied according to the desired pH values of the solutions. The results are shown in Figure 6.

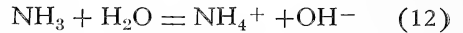
The soil adsorbed about the same amount of sodium and ammonium ions up to pH 7 with acetate solutions. The amount of sodium ions adsorbed beyond pH 7 increased rapidly with increase in pH, while the amount of ammonium

ions adsorbed tended to level off beyond this point. Adsorption from NH_4Cl and NH_4OAc solution followed similar patterns, but adsorption from the latter was significantly greater. The influence of anions on the amount of cation adsorbed by clays is well known, but as yet there seems to be no adequate explanation. Iimura (1961) showed that the amount of ammonium ions adsorbed increased with pH, following the same pattern of sodium adsorption by allophanic clays obtained in this study. The discrepancy seems to be due to the difference in the experimental procedures employed. His procedure was essentially that of Schofield (1949), under whose method the amount of ammonium ions adsorbed was determined without the removal of the excess salt present, while in the procedure used in this study excess salt was removed by alcohol and the ammonium ions adsorbed were apparently removed as the excess salt was removed from the system. This may be explained as follows:

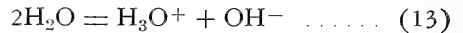
Since the hydronium ion activity is very low in a solution having a pH of 8 and above, the following equilibrium tends to shift to the right:



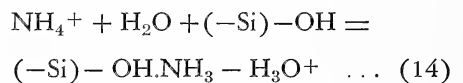
When protons of the silanol groups are replaced by ammonium ions, the ammonium ions will be strongly polarized so that they will split more or less distinctly into ammonia molecules and protons, the protons being strongly attracted toward the oxygen atoms on silicon atoms. Considering the equilibria



and



with equilibrium constants of 1.8×10^{-5} and 10^{-14} , respectively, the equilibrium constant for (11) will be $10^{-14}/1.8 \times 10^{-5} = 5.6 \times 10^{-10}$. The equilibrium constant for the equilibrium



is less than 10^{-8} , as can be seen by comparing the results in Figure 6 with those in Figure 1. It may be concluded that the ammonium ions

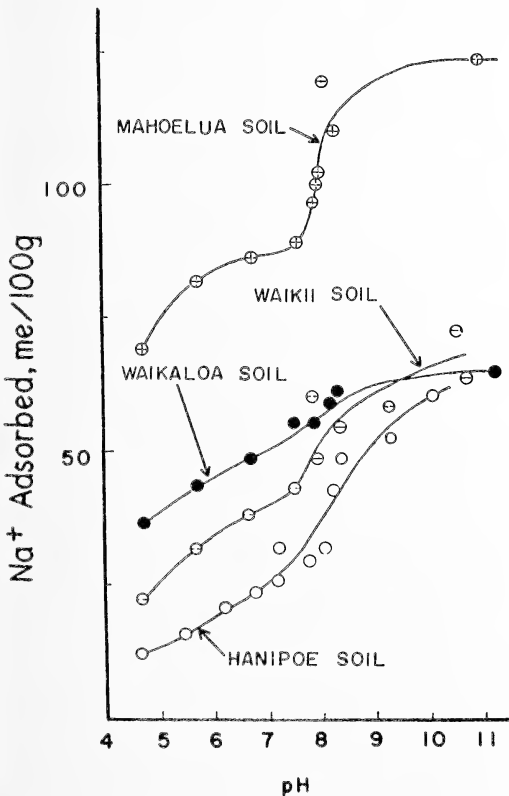


FIG. 4. Exchange curves of allophanic soils. \circ , Hanipoe soil; \odot , Waikii soil; \oplus , Mahoelua soil; and \bullet , Waikaloa soil.

TABLE 1
COMPOSITION AND CEC OF SYNTHETIC GELS (AIR-DRIED BASIS)*

	A ₁	A ₂	B ₁	B ₂	B ₃	B ₄
SiO ₂	8.99	30.82	32.51	41.58	46.53	48.38
Al ₂ O ₃	24.92	22.96	20.72	12.54	9.46	7.48
H ₂ O (LOI)	11.86	7.64	6.69	6.88	5.86	5.07
H ₂ O—	47.03	25.89	27.64	29.21	30.87	34.18
Total	92.80	87.31	87.56	20.21	92.54	95.11
Na ₂ O (by difference)	7.20	12.69	12.44	9.79	7.46	4.89
Si/Al	0.306	0.671	1.382	2.814	4.159	5.487
CEC(me./100 g)	245	455	420	292	190	120
CEC/Al	0.501	1.01	1.03	1.19	1.02	0.82
Approx. inflection point, pH	6	5	5	6 and 4	4	4

* Analyst, Mr. H. Tenma.

held on the silanol groups are in fact partly ammonium ions and partly ammonia molecules. The equilibrium in (14) is strongly favored to the left, and, as excess ammonium ions are removed from the equilibrium system, ammonia is liberated into the washing alcohol, dissolving in it as ammonia molecules. This is quite dif-

ferent from the loss due to hydrolysis, in which cations are lost by replacement with protons produced by the dissociation of the dispersing medium, usually water. Dissociation of sodium ions into the washing alcohol seems to be prevented, probably because the proton activity in alcohol is too small to cause hydrolysis.

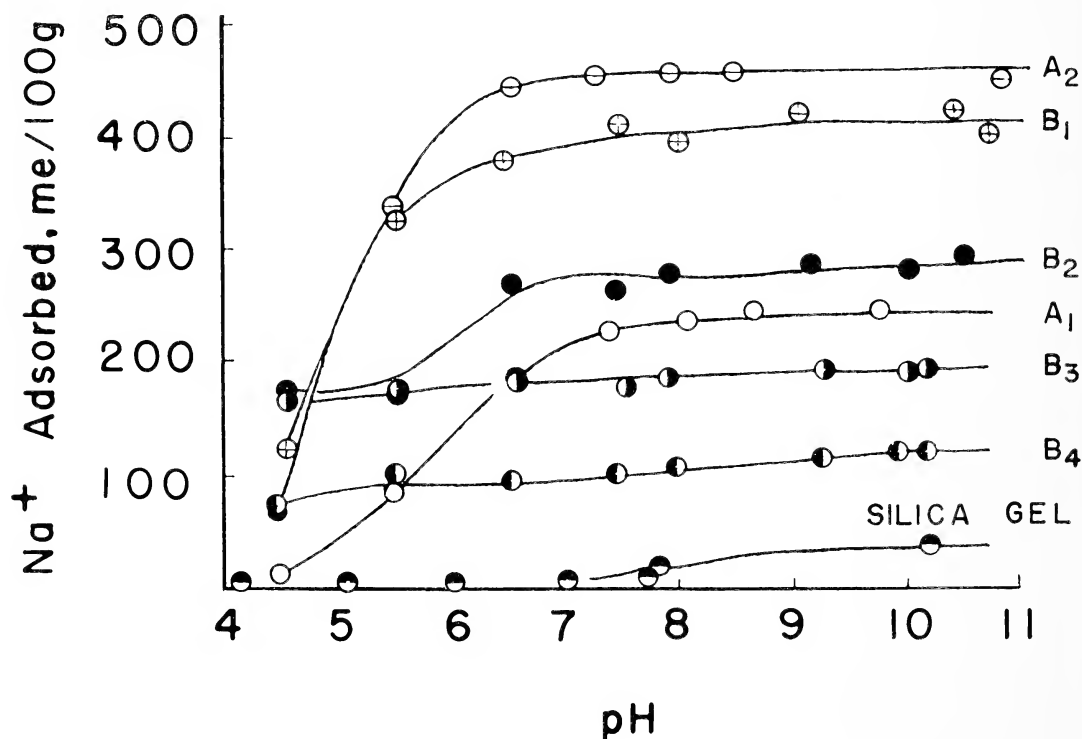


FIG. 5. Exchange curves of synthetic aluminosilicate gels and a silica gel. From top, A₂ (⊖), B₁ (⊕), B₂ (●), A₁ (○), B₃ (⊙), B₄ (⊖) and silica gel (⊙).

It may be considered that the pH-dependent charges produce strong polarizing effect on hydronium ions, so that the protons are detached from the water molecules and bonded to the oxygen atoms of the aluminosilicate exchanger, forming hydroxyl groups. Permanent charges are not polarizing, so that hydronium ions neutralizing them remain as such in the system. Therefore, the hydronium ions on the permanent charge sites can be readily replaced by other cations, but the protons on the silanol groups are not so easily replaced. In this connection, it may be considered that the charges arising on the surface of the exchanger will have a stronger polarizing effect on the hydronium ions, while the charges arising inside the exchanger will have a weaker polarizing effect. The charges due to the broken bonds and surface hydroxyls will be pH-dependent, and the charges due to isomorphous replacement can be pH-dependent or permanent, depending on the distance from the surface of the exchanger to the site where the isomorphous replacement takes place. Here, permanent charges can be defined as the charges which do not give strong polarizing effect on neutralizing ions, and the pH-dependent charges are those which give strong polarizing effect on the neutralizing ions.

It may be concluded that the charges of the allophanic clays of the soils studied are due mostly to the surface silanol groups and tetrahedrally-coordinated aluminum atoms. The former charges show weak acidic character, the latter strong acid character. Contribution of the hydroxyl groups of aluminum hydroxide to the total exchange capacity seems to be insignificant.

It is quite unlikely that the silanol groups of the soil colloids will contribute to cation exchange of a soil under natural conditions, except in saline and alkaline soils. It is considered more desirable for most practical purposes to express cation exchange determinations in terms of permanent charges.

SUMMARY

1. Cation exchange in soils is considered to be an equilibrium reaction between the clay acid and the clay salt, assuming that the hydrogen-saturated and metal ion-saturated clays

behave as if they were weak acid and salt, respectively.

2. Comparisons of the exchange curves obtained on clay minerals, allophanic clays, soils, and on synthetic silica, aluminosilicate, and aluminum hydroxide gels indicated that the so-called pH-dependent charges of the clays were most likely due to the dissociation of surface hydroxyl groups associated with silicon atoms (silanol groups), and that the so-called permanent charges were due to isomorphous replacement. In synthetic gels and the allophanic clays, the permanent charges were most probably due to tetrahedrally coordinated aluminum atoms in the aluminosilica network.

3. The lower exchange capacity obtained with NH_4^+ ions at higher pH values is explained on the basis that competition of protons between the pH-dependent charges and the ammonia molecules resulted in dissociation of NH_4^+ ions to protons and ammonia molecules,

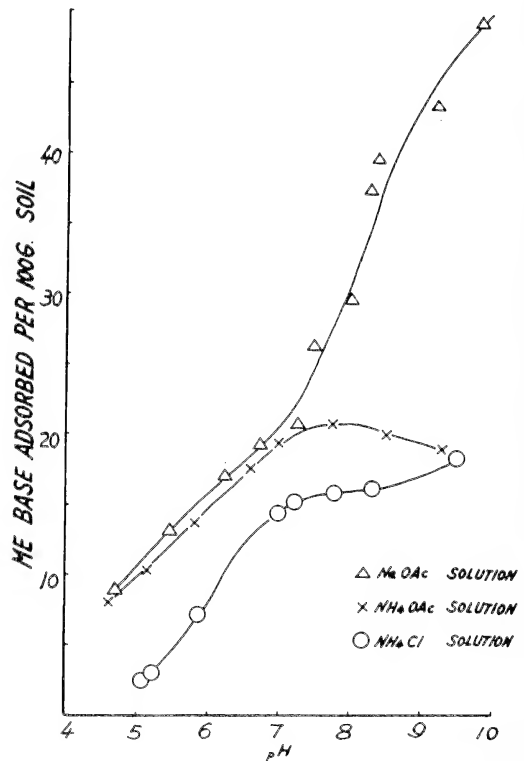


FIG. 6. Exchange curves of Hanipoe soil using different saturation solutions.

which resulted in the loss of ammonia upon removal of the excess salt.

4. It is suggested that the amount of exchangeable bases should be expressed in terms of percentage of the permanent charges, since the pH-dependent charges were considered not to take part in the exchange reaction under normal soil conditions.

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NOTES

Notes on the Coloration and Behavior of the Common Dolphin, *Coryphaena hippurus*

A. EARL MURCHISON and JOHN J. MAGNUSON¹

WHILE STUDYING scombrid fishes at the Kewalo Basin tank facility of the U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, we noted similarities between the behavior of the common dolphin, *Coryphaena hippurus* Linnaeus, and that of the scombrids. These similarities led us to observe the coloration, swimming speed, and behavior of *C. hippurus* incidentally to the studies on scombrids.

Most observations were made on five captive specimens in shoreside tanks during July–September 1962. Additional observations were made at sea through underwater viewing ports from a raft.

The *C. hippurus* specimens had been caught by trolling with barbless hooks, transported in a baitwell of a commercial fishing boat, and transferred at shore by dip net to a portable 2300-l tank from which they were allowed to swim directly into the shoreside tank in the manner described by Nakamura (1962, *Copeia* 1962 (3):449–505). The outdoor tank was circular, 24 ft in diameter, and 3½ ft deep, and had an observation window in its wall. Water temperature in the tank was about 24° C during the day and 22° C at night. Salinity was 33‰.

All five fish eventually jumped out of the tank and died, the last after 45 days in captivity.

The *C. hippurus* averaged 76 cm in fork length and 3.7 kg in weight. They were fed 5–7-gm pieces of beef liver and whole thawed night smelt, *Spirinchus starksi* (Fisk), which weighed approximately 12 gm. When fed at 24-hr intervals, the fish ate 334 gm per feeding, approximately 9% of the body weight.

Although *C. hippurus* have been reported

by many authors to exhibit a changing array of many brilliant colors, their basic coloration in the tanks and at sea varied between two extremes. One was a silver-blue phase similar to that illustrated by the Fisheries Society of Japan (1931, *Illustrations of Japanese Aquatic Plants and Animals*, I, Pl. XXX). The other extreme was a yellowish phase similar to that illustrated by Walford (1937, *Marine Game Fishes of the Pacific Coast, Alaska to the Equator*, Univ. Calif. Press, Berkeley, Pl. 43) and noted by Gibbs and Collette (1959, *Bull. Mar. Sci. Gulf Carib.* 9(2):122) and Rothschild (1964, *Copeia* 1964 (2):445–447). Intermediate shades between these two extremes occurred. The intermediates were various hues of greenish-blue or greenish-yellow and apparently resulted from the combined effects of the blue and the yellow coloration.

In the extreme silver-blue phase the body and caudal fin were silver-blue. The extreme ventral body surface was silver-white. The dorsal fin, the dorsal surface of the pectoral fins, and the lateral surfaces of the pelvic fins were blue. Dark blue spots 3–5 mm in diameter were scattered over the body.

In the extreme yellow coloration, more evident at sea than in tanks, the caudal fin, the anal fin, the outer surface of the pelvic fins and the dorsal surface of the pectoral fins turned bright yellow while the head and body turned greenish-yellow. The same dark-blue spots were present.

C. hippurus observed through underwater viewing ports from a raft, *Nenue*, described by Gooding² tended to take on the yellow coloration just after reacting to food or just after a transient barred coloration described below

¹ U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii 96822. Manuscript received May 18, 1965.

² Gooding, Reginald M. 1965. A raft for direct subsurface observations at sea. U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 517. 5 p.

faded. The yellow coloration also occurred while *C. hippurus* were struggling on a hook and line or lying on the deck just after capture.

The broad dark vertical bars described by Strasburg and Marr (1961, Copeia 1961 (2): 226–228) were observed in the tank only once and then they were faint. These alternate dark and light vertical bars about 5 cm wide formed on the lateral surfaces of the *C. hippurus* when a live 25-cm *Tilapia mossambica* was tossed into the tank after the *hippurus* had not been fed for 10 days. The bars were displayed during an attack by the *hippurus* which ended with the consumption of the *T. mossambica*. A more prominent barred coloration was observed at sea after chopped meat was tossed in front of two *hippurus* swimming around the observation raft, and while the *hippurus* were attacking species of smaller fishes congregated at the raft.

The *hippurus* in the tanks swam continuously day and night with an undulating body movement, mouth agape and pectoral fins extended. During turns of 90° or sharper, the dorsal fin was raised slightly. The left pelvic fin was extended during gradual left turns; the right during gradual right turns. The typical swimming speed of a 71.1-cm *hippurus*, measured on three different days over a one-week period, was 56.3 cm/sec (0.79 body length/sec) (95% confidence interval: 54.8–57.8 cm/sec; $n = 31$ 30-sec observations, $s^2 = 19.32$). At this speed approximately 50 km would be traversed in a 24-hr period. The typical tail-beat frequency was 1.21 beats/sec (95% confidence interval: 1.10–1.32 beats/sec; $n = 31$, $s^2 = 0.09256$). A tail beat is defined as a complete cycle back and forth. At the typical speeds the fish was moving 46.5 cm/tail beat or 0.654 body length/tail beat. Motion pictures taken from the raft showed the average tail-beat frequency of *C. hippurus* about 100 cm in fork length swimming near the raft to be 1.20 beats/sec (95% confidence interval: 1.14–1.27 beats/sec; $n = 8$, $s^2 = 0.009143$), essentially the same as in the tank. The surface temperature was 27° C, only 3° C higher than the daytime tank temperatures.

These slow rates of swimming are those most commonly observed for *C. hippurus* both in tanks and at sea. Since they never stop swim-

ming, these are as close to resting speeds as the animal attains. These dolphins apparently irrigate their gills by forward progression through the water and maintain swimming depth by the hydrodynamic lift exerted against the pectoral fins. They do not have a gas bladder. These same functional components (respiration and hydrostatic equilibrium) of locomotion in pelagic fishes have been noted previously for scombrids (Breder, 1926, Zoologica 4(5):159–297; Hall, 1930, Am. J. Physiol. 93(2):417–421; Magnuson and Prescott³, Nakamura, op. cit.) and are probably a very common adaptation of locomotion in pelagic fishes.

Several characteristic behavior patterns were observed among the *C. hippurus* in captivity. These were named mouth closure, oral valve closure, yawn, lean, chafe, jerk, and defecation. All of these, plus surfing, also were observed at sea. Their occurrence both in captivity and at sea suggests that they are naturally occurring behavior patterns in the repertoire of *C. hippurus*. A brief description of each, based primarily on the tank observations, is presented here.

Mouth closure. The mouth is closed completely for 1–5 sec and then reopened to the typical 2- to 5-cm gape.

Oral valve closure. For periods of less than 1 sec, the mouth is closed partially from the typical gape in such a way that the oral valve appears to close completely. The mouth then is reopened to the typical gape.

Yawn. The mouth is opened maximally, the gular region is depressed, the opercles are flared, all fins are extended, and all caudal motion is stopped. Typical posture and locomotion are disrupted for 3–4 sec.

Lean. The body is tipped to the side at angles of 45–90°. Sometimes this results during a turn as a continuation of a banking posture, but occasionally it results from a quick tipping movement while following a straight course. Then the dorsal fin is extended, as are the pectoral and pelvic fins on the side toward the surface.

³ Magnuson, John J., and John H. Prescott. 1966. Courtship, locomotion, feeding and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14(1):54–67.

This swimming posture is maintained for 3–10 sec and ends with a sudden return to the upright swimming posture.

Chafe. While swimming past an object, the fish brushes or rubs the lateral body surface against the object. If the chafe is directed against the tank's standpipe or sides, the normal upright swimming posture is maintained, but if the object chafed against is above the dolphin, the chafe occurs in conjunction with a lean.

Jerk. A single shudder or quiver passes over the body without visibly affecting locomotion.

Defecation. A brownish-green cloud of fine material was ejected for a 1–3 sec period during typical swimming behavior.

Surfing. The fish swims downwind just beneath the surface, positioning itself in front of a wave crest. The anterior-posterior axis of the

body is inclined from the horizontal at approximately the same angle as the lead surface of the wave. With little or no caudal movement the fish travels rapidly forward in a horizontal plane at the same speed as the wave crest.

The mouth closure, yawn, lean, and jerk of *C. hippurus* appear very similar to patterns observed in another pelagic fish, the Pacific bonito *Sarda chiliensis* (Cuvier) (Magnuson and Prescott, op. cit.). Other similarities are the transient vertically barred coloration, shared also with the skipjack tuna, *Katsuwonus pelamis* (Linnaeus) (Nakamura, op. cit.), and continuous swimming. These similarities in behavior between a coryphaenid and a scombrid suggest that the functions may also be the same and are perhaps common to many pelagic predaceous fishes.

Echinoderes arlis, a New Kinorhynch from the Arctic Ocean

ROBERT P. HIGGINS¹

THE FIRST KINORHYNCH to be reported from within the Arctic Circle was *Centroderes arcticus* (Steiner, 1919) new combination. This species was originally described in one of several invalid "larval genera," the genus *Centropsis* Zelinka, 1907. Steiner's description is such that if a closer study were possible his species might be better assigned to the genus *Campyloderes* Zelinka, 1907, the only other genus in the family Centroderidae Zelinka, 1907.

The family Echinoderidae Bütschli, 1876 has been reported from as far north as Bergen, Norway (Schepotieff, 1907:134) and the northern Baltic Sea (Levander, 1900:19; Karling, 1954:189). The southernmost limit of this family's distribution is South Georgia Island in the southern Atlantic (Lang, 1949:17). Members of the single genus within this family, *Echinoderes* Claparède, 1863, are widely distributed and are very common representatives of the phylum Kinorhyncha.

The species described in this paper is the first member of the genus *Echinoderes* reported from within the Arctic Circle and is from the greatest recorded depth for the phylum.

Genus *Echinoderes* Claparède, 1863

Echinoderes arlis n. sp.

Figs. 1 and 2

DESCRIPTION: Holotypic female, 420 μ trunk length (trunk length measured between anterior margin of segment 3 and posterior margin of segment 13); msw-10, 85 μ (maximum sternal width at segment 10—a measurement across the anterior margin of widest sternal plates); sw-12, 70 μ (sternal width at segment 12—a similar measurement); trunk length—msw ratio 4.9:1, trunk length—sw-12 ratio 6.0:1.

Second segment with 16 anteriorly rounded

placids, midventral placid truncate, distinctly larger than others; trichoscalid plates not observed.

Trunk segments (segments 3–13) with numerous hairs, often very long, up to 17 μ , pattern distinctive (Figs. 1 and 2).

Posterior border of each trunk segment with pectinate fringe except for terminal tergal plate.

Middorsal spines long, on segments 6, 8, and 10, 73 μ , 92 μ , and 125 μ ; lateral spines on segments 8–11, all approximately 42 μ in length; accessory lateral spines of segment 13, 67 μ in length, 0.32 \times the lateral terminal spines; lateral terminal spines 210 μ in length, 0.50 \times the trunk length.

Posterior margin of terminal tergal plate deeply incised, forming broadly rounded margins which abruptly form elongate spinous projections (Figs. 1 and 2); sternal plates of terminal segment with broadly rounded margins positioned anterior to the limits of the tergal margin.

Pachycycli (thickened anterior margins of the trunk segments) well developed; muscle scars prominent only on medial portion of twelfth sternal plates.

Pigmented eye-spots not noted due to preservation; adhesive tubes 20 μ in length, on ventral surface of segment four, directly anterior to tergal-sternal junction of fifth segment.

Allotypic male, 382 μ trunk length; msw-10, 73 μ ; sw-12, 65 μ ; trunk length—msw ratio 5.2:1, trunk length—sw-12 ratio 5.9:1; flexible penis spines 20 μ in length, originating from anterolateral margin of terminal sternal plates; accessory lateral spines 40 μ in length, shorter than those of female; lateral terminal spines longer than in female, 238 μ in length, 0.62 \times trunk length.

The range in trunk length for all females examined was 380–420 μ ; all but the holotype were mounted laterally, preventing further range measurements concerning width. Lateral terminal spines measured 210–224 μ in length,

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0.50–0.59 \times the trunk length; lateral accessory spines measured 67–80 μ in length, 0.28–0.32 \times the lateral terminal spine length; middorsal spines of segments 6, 8, and 10 measured 73–76 μ , 92–110 μ and 115–126 μ in length; lateral spines were more nearly equal in length, measuring 34–45 μ .

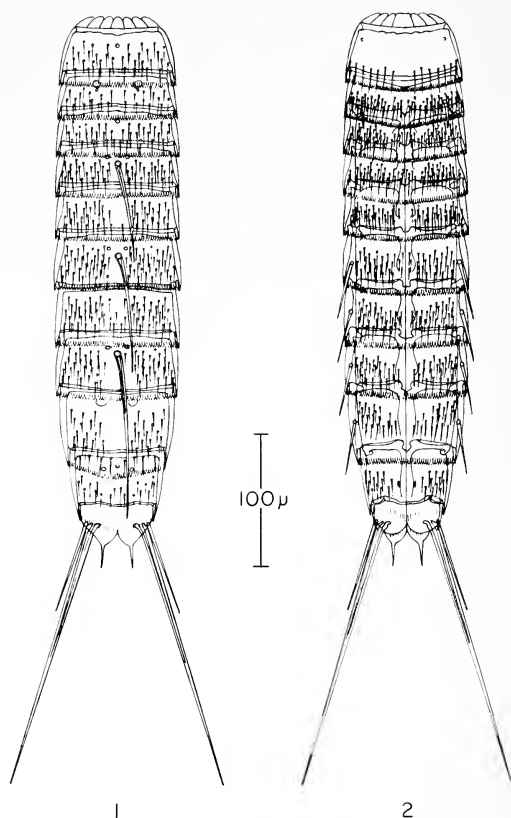
The range in trunk length for all males examined was 382–420 μ ; the maximum sternal width occurred at segment 10 and measured 73–80 μ , giving a trunk length–msw ratio of 5.2:1 in all males. The sternal width at segment 12 measured 65–71 μ , giving a trunk length–sw-12 ratio of 5.9:1 in all males. Lateral terminal spines measured 230–238 μ in length, 0.55–0.62 \times the trunk length; the lateral accessory spines were measured only in the allotype; middorsal spines of segments 6, 8, and 10 measured 79–89 μ , 98–105 μ and 105–115 μ in length; lateral spines were more nearly equal in length, measuring 33–44 μ .

TYPE LOCALITY: 74.5° N, 163.9° W, from a depth of 747 m.

MATERIAL EXAMINED: Six specimens; four females and two males. Holotypic female (author's number K 57.1) and one other female from type locality, station 360, Arctic Research Laboratory Ice Station 1 (ARLIS-1, from which the species name is derived), off Point Barrow, Alaska, collected by John Tibbs, 16–17 January 1961. Allotypic male (author's number K 58.4) one other male and two females from station 446 (74.8° N, 165.6° W), ARLIS-1, collected by John Tibbs, 9–10 February 1961, from a depth of 419 m.

DISPOSITION OF TYPES: Holotypic female (USNM 32924), and allotypic male (USNM 32923) have been deposited in the marine invertebrate collection of the U. S. National Museum. The remaining paratypes are in the author's personal collection.

REMARKS: *Echinoderes arlis* n. sp. is within the size limits of several species including *E. pilosus* Lang, 1949, *E. bengalensis* (Timm, 1958), *E. pennaki* Higgins, 1960, and *E. brevispinosus* Higgins, 1966, but differs from these by having elongate middorsal spines on segments 6, 8, and 10. Only one species, *E. riedli* Higgins, 1965, has the same middorsal spine arrangement and this is a very small



FIGS. 1 and 2. *Echinoderes arlis* n. sp., holotypic female, neck and trunk segments (head retracted). Fig. 1, dorsal aspect; Fig. 2, ventral aspect.

species, 228 μ in length, recently described from the Red Sea.

The lateral spination of *E. arlis* n. sp. is shared by *E. setigera* Greeff, 1869, *E. pilosus* and *E. levanderi* Karling, 1954, but other than for *E. setigera*, whose middorsal spines are on segments 6, 7, and 9, the remainder have a full complement of middorsal spines on segments 6 through 10.

In addition, *E. arlis* n. sp. differs from all other members of this genus by the shape of the terminal border of segment 13.

ACKNOWLEDGMENTS

I am grateful to Dr. John L. Mohr, Dr. Stephen R. Geiger, and Dr. John Tibbs, University of Southern California, for their generosity in providing the specimens. The specimens were collected with support by contract

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Paper Electrophoresis Patterns of Sera from Seven Genera of Decapod Crustaceans

LAWRENCE D. HUGHES¹ and LINDSAY R. WINKLER²

ABSTRACT: The pattern noted for the various families was simple, showing one major protein band and, in most cases, at least one minor one. Serum from crabs from the open coast always showed two bands, while those from the mud flats showed but one. This held even in *Pachygrapsus*, which is found in both habitats.

RECENTLY Woods et al. (1958) reported a very close similarity in the electrophoretic patterns in starch gel of related species of crabs, and stated that, not without exceptions, such electrophoretic relationships seemed to extend to the family level. This work prompted the authors to do a cursory study of representatives of a number of the families of crabs common to the southern California coast.

Paper electrophoresis rather than starch gel was used, employing the Spinco Model R electrophoresis apparatus to separate the serum proteins of specimens from eight genera of decapod crustaceans, representing seven families. The separations were made on individual samples, and, in the case of the smaller species, on pooled samples in a veronal buffer at pH 8.6 with an ionic strength of .075. The liquid sera were separated from the clot and applied to the paper strips and run at 5 milliamperes for 16 hr. Since only the Grapsidae were represented by more than one genus, no generalization can be made as to uniformity within the families.

Differences noted among the families included (a) rapidity of migration of the major band, (b) relative migration of the minor band, (c) strength of the two bands both relative and absolute, and (d) the appearance of a third band in the case of the *Pleuroncodes* (Galatheidæ) (Fig. 1, E.). This latter may be of significance in view of the uncertain taxonomic position of the Galatheidæ, and, if it is found to be a consistent characteristic in large numbers

of specimens, might easily be construed to support a more distant relationship with the main body of the crabs.

However, there appears to be an environmental as well as a genetic relationship in the electrophoretic patterns of the serum proteins of these animals. It will be noted from Figure 1 that those forms which are more commonly associated environmentally tend to have a broad similarity in their electrophoretic patterns. This environmental pattern is shown to exist even within the species in the case of *Pachygrapsus crassipes* Randall which, in Southern California, lives on the margins of the mud flats as well as in the rocky intertidal zone of the open coast.

All the crabs living in the open water (Fig. 1, A-E) and on the well aerated tidal zones, including *P. crassipes* (Grapsidae), show two well-defined protein components, whereas all those (again including *P. crassipes*) taken from the muddy shores (Fig. 1, F-H), where routinely there are wide variations in the tides and high salinity-low oxygen relationships, have but one protein component.

The food supply available to these two environmental groups of crabs also differs widely. The former group has abundant supplies of red, brown, and green algae, as well as various forms of animal life. The second group, living on the mud flats, has a much more limited food supply, consisting of small green algae and saline higher plants, supplemented by more limited amounts of animal and plant material. In addition, the population levels of *P. crassipes* on the beaches studied were much lower than they were on the muddy shores, which may have been a significant influence in the latter group.

The almost identical patterns of *Hemigraps-*

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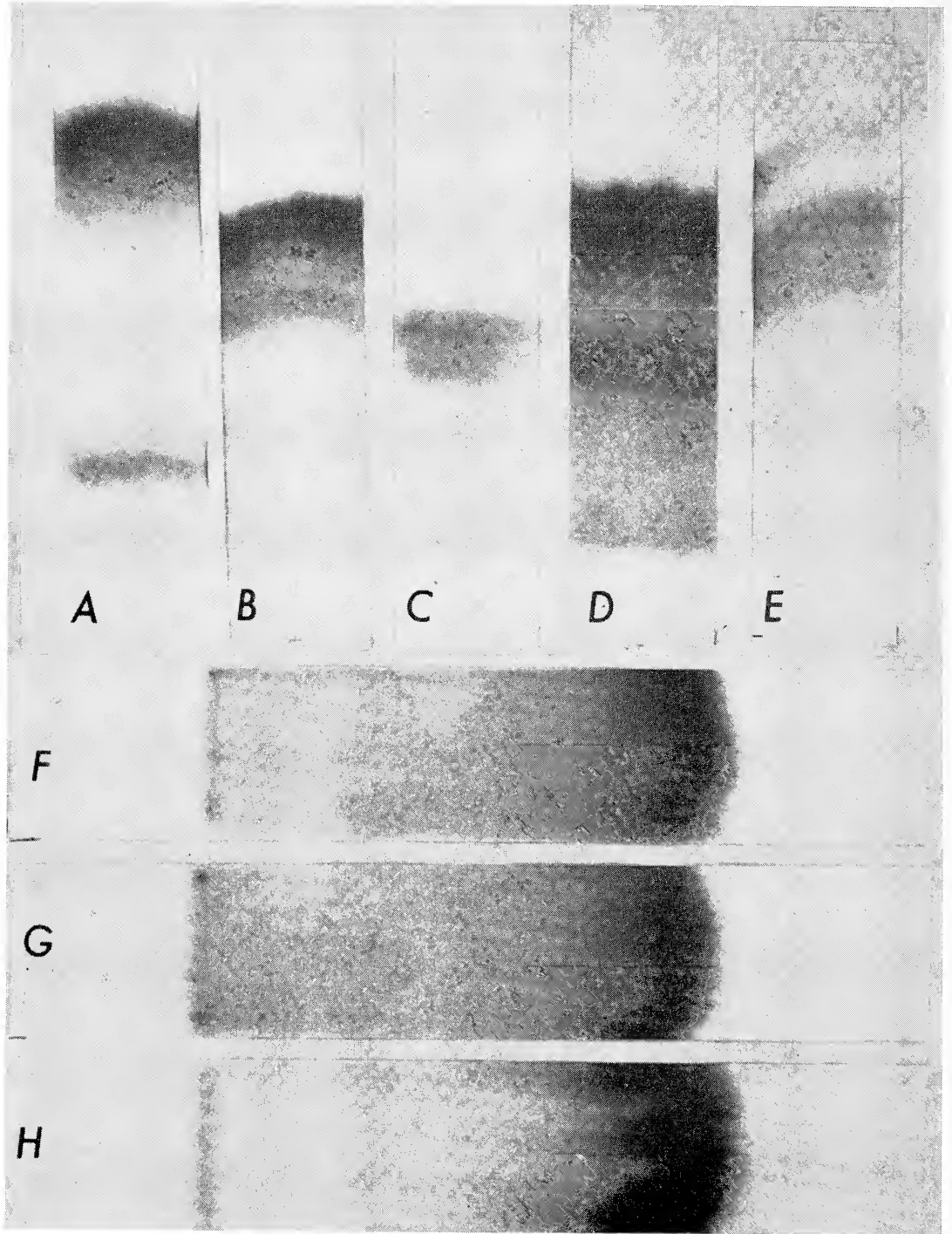


FIG. 1. A-E, Electrophoretic patterns of sera from crabs from tidal zone and open water. F-H, Electrophoresis patterns of sera from crabs from mud flats. A, *Portunus* (Portunidae); B, *Pachygrapsus* (Grapsidae); C, *Cancer* (Cancridae); D, *Loxorhynchus* (Majidae); E, *Pleuroncodes* (Galatheididae); F, *Hemigrapsus* (Grapsidae); G, *Pachygrapsus* (Grapsidae); H, *Uca* (Ocypodidae).

sus, *Uca*, and *Pachygrapsus* from the mud flats would seem to indicate a strong environmental or nutritional influence on the electrophoretic pattern of the blood proteins synthesized, superimposed on the species-controlled genetic factor. This hypothesis is strengthened by the obvious difference, within the species *P. crassipes*, between specimens living in the two different environments mentioned (Fig. 1, *A-E* and 1, *F-H*).

Work in progress toward experimental elucidation of this blood pattern difference in

Pachygrapsus, using the more sensitive agar gel electrophoresis, seems to indicate that the nutritional factor may be the predominant influence in the environment. The results of these studies will be reported upon completion.

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Dry-Wood Termite Attacks in a 55-Year-Old Display of Hawaii-Grown Wood

R. SIDNEY BOONE¹

ABSTRACT: Display racks built in 1909 to exhibit various woods grown in Hawaii provided some unique observations on dry-wood termite infections. Of 79 wood samples, including 76 species, 54 samples were not attacked. It is quite likely that this may be the only record of dry-wood termite resistance for many of these species.

AS THEY ARE in most tropical areas of the world, dry-wood termites (*Cryptotermes brevis* Walker) are a serious problem in Hawaii. These insect pests differ from subterranean termites in that they live entirely in wood, never enter the ground, and require but little moisture for existence. Established colonies of subterranean termites normally maintain contact with the ground—usually in the form of earthen tunnels—for their constant supply of moisture. Colonies of dry-wood termites grow slowly.

¹ Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Honolulu, Hawaii. Manuscript received October 21, 1965.

They are usually much smaller than colonies of subterranean termites. Dry-wood termites can attack wood with a moisture content as low as 10–12% and possibly even lower (Hunt and Garrett, 1953:53). Consequently they are found in the upper structural parts of houses, telephone and utility poles, furniture, fiber insulation board, pianos, paper, and other wood products having a low moisture content.

Three display racks built in 1909 provided us with some unique observations on dry-wood termite infestations. They were built to exhibit various woods grown in the Hawaiian Islands. In 1910 they won a gold medal at the Alaska-Yukon-Pacific Exposition in Seattle. Since then,

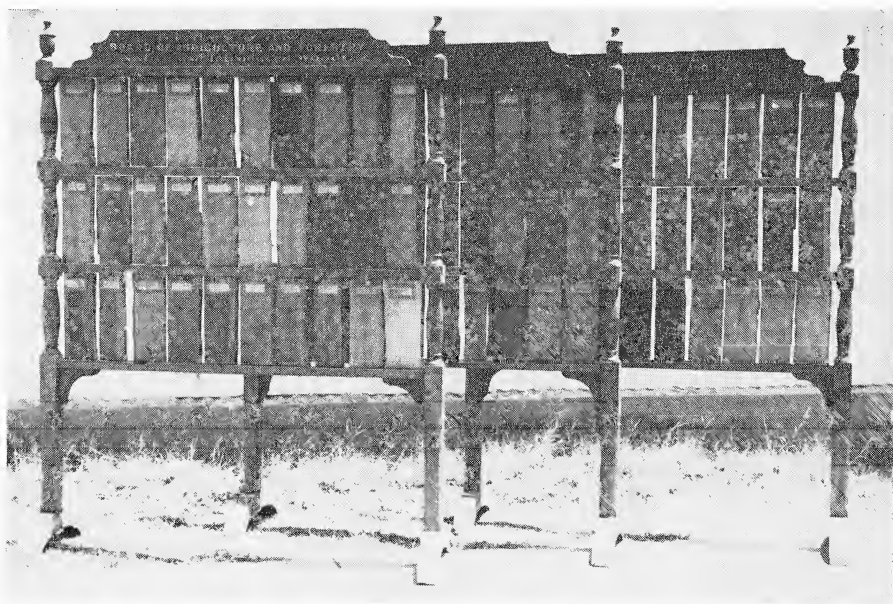


FIG. 1. Display racks in 1965.

TABLE 1
DRY-WOOD TERMITE ATTACKS IN HAWAII-GROWN WOOD

SCIENTIFIC NAME ¹	COMMON NAME	NONE	TERMITE ATTACK		SEVERE	SAMPLES FIT SNUG- LY IN RACK	TERMITES IN RACK ADJACENT TO SAMPLES
			OCCA- SIONAL	MOD- ERATE			
<i>Acacia koa</i> Gray	koa	x	-	-	-	-	x
<i>Acacia koa</i> Gray	koa	x	-	-	-	-	-
<i>Acacia koa</i> Gray	koa	-	x	-	-	x	x
<i>Acacia koa</i> Hbd.	koaia	x	-	-	-	-	-
<i>Acacia melanoxylon</i> R. Br.	blackwood acacia	x	-	-	-	-	-
<i>Albizia lebbek</i> Benth.	siris-tree	-	x	-	-	x	x
<i>Aleurites moluccana</i> Willd.	kukui	x	-	-	-	-	-
<i>Alphitonia ponderosa</i> Hbd.	kaula	x	-	-	-	-	-
<i>Anidesma platyphyllum</i> Mann	hame	-	x	-	-	-	-
<i>Artocarpus altilis</i> L.	breadfruit	-	-	-	-	-	-
<i>Bobea mannii</i> Hbd.*	ahahea	-	-	-	x	x	x
<i>Byrsonia sandwicensis</i> Endl.*	aiea	x	-	-	-	-	-
<i>Caesalpinia sappan</i> L.*	sappan	x	-	-	-	-	-
<i>Calophyllum inophyllum</i> L.	kamani	-	-	x	-	x	x
<i>Cantium odoratum</i> F.V.M.	alahae	x	-	-	-	-	-
<i>Ceiba pentandra</i> L.	kapok	x	-	-	-	-	-
<i>Cheirodendron gaudichaudii</i> Seem	olapa	x	-	-	-	x	-
<i>Cheirodendron gaudichaudii</i> Seem	olapa	x	-	-	-	x	-
<i>Citrus aurantium</i> L.*	orange	x	-	-	-	x	-
<i>Cocos nucifera</i> L.	coconut	-	x	-	-	-	x
<i>Cordia subcordata</i> Lam.	kou	-	-	-	-	-	-
<i>Coprosma longifolia</i> Gray*	pilo	-	x	-	-	-	-
<i>Coprosma waimaeae</i> Wawra*	olena	x	-	-	-	x	-
<i>Cryptocarya mannii</i> Hbd.	holio	x	-	-	-	-	-
<i>Diospyros ferrea</i>	lama	x	-	-	-	x	-
<i>Dracaena aurea</i> Mann	hala-pepe	x	-	-	-	-	-
<i>Dubautia plantaginea</i> Gaud.*	naenae	-	x	-	-	-	-
<i>Elaeocarpus bifidus</i> Hook. et Arn.	kalia	-	x	-	-	-	-
<i>Erythrina sandwicensis</i> Degener	wiliwili	x	-	-	-	-	-
<i>Eucalyptus calophylla</i> R. Br.	Port Gregory eucalyptus	x	-	-	-	-	-
<i>Eucalyptus citriodora</i> Hook. ²	lemon eucalyptus	x	-	-	-	x	-
<i>Eucalyptus globulus</i> Labill.	bluegum eucalyptus	x	-	-	-	-	-
<i>Eucalyptus goniocalyx</i> F. Muell.	mt. graygum eucalyptus	x	-	-	-	-	-
<i>Eucalyptus gummifera</i> Hochr.	bloodwood eucalyptus	x	-	-	-	-	-
<i>Eugenia cumini</i> L.	Java plum	x	-	-	-	x	x
<i>Eugenia malaccensis</i> L.	mountain apple	x	-	-	-	x	-
<i>Eugenia sandwicense</i> Ndz.	ohia ha	x	-	-	-	x	-
<i>Euphorbia longana</i> (Lour.) Steud.	longan	x	-	-	-	-	x

the racks have been displayed or stored in various parts of Honolulu, always in areas accessible to dry-wood termites.

Almost nothing is known about the resistance of many Hawaii-grown woods to dry-wood termite attack. All observations that may give some indication of differences in resistance are desirable. These display racks gave us such an opportunity for samples of 76 wood species.

Woods for the display were collected throughout the islands by J. F. Rock, territorial botanist. The racks were built of koa. Each rack held 30 specimens (Fig. 1). Each specimen measured 1 by 5 by 12 inches. The bark was exposed on one edge. The specimens were mounted with metal rods, extending about $\frac{1}{2}$ inch into the top and bottom, allowing them to rotate in the rack. A label on the sample showed the common and scientific names. Of the original 90 wood samples, 79 specimens, including 76 species, are still labeled and identifiable. Only 2 specimens are missing, and 9 others have lost their name plates (Fig. 1).

In 1965 each specimen block was carefully inspected from all sides and all angles. They were not removed from the rack nor were cuts made in them. In two specimens the termites were still active. No information is available as to the age of any colony or how quickly an infested specimen was damaged.

Termite attack was arbitrarily divided into four classifications: none (no holes); occasional (1–3 holes); moderate (3–10 holes); and severe (completely riddled, in some only a shell left). There was no difficulty in deciding on the proper category for a given sample.

Of the 79 specimens, only 25 were attacked by the dry-wood termites (Table 1). Of these, only 7 were severely attacked, 4 had moderate attack, and 14 had occasional attack. The remaining 54 specimens were not attacked.

In some instances, the attack or lack of it was not in keeping with published data or local experience. Koa, for example, is known to be subject to attack, and the koa racks were infested. But only 1 of the 3 samples of koa showed attack. On the other hand, ohia is be-

lieved to be resistant, and yet the sample of ohia showed an occasional attack.

Termite attacks were found more often in those samples that fitted rather tightly in the frame, that is, they touched the frame at either the top or bottom. But several samples that fitted snugly were not attacked. Because all samples originally had bark, there was equal opportunity for termites to enter between the bark and sapwood.

An attempt to segregate attacks as being in sapwood or heartwood was unsuccessful. Many of the samples had no heartwood owing to the smallness of the tree from which they came. On most of the light colored woods it was impossible to separate heartwood and sapwood owing to discoloration from weathering.

Quite likely this may be the only record of dry-wood termite resistance for many of these species in Hawaii. Although these samples have not been observed periodically over the years for termite damage, their exposure for more than 50 years in areas known to have dry-wood termites should provide some definite signs of their susceptibility to insect attack. A controlled experiment would be a more desirable way of studying this problem, but it is doubtful that this will be done because many of these tree species have little or no economic value.

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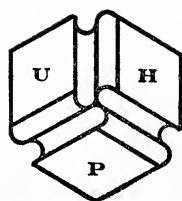
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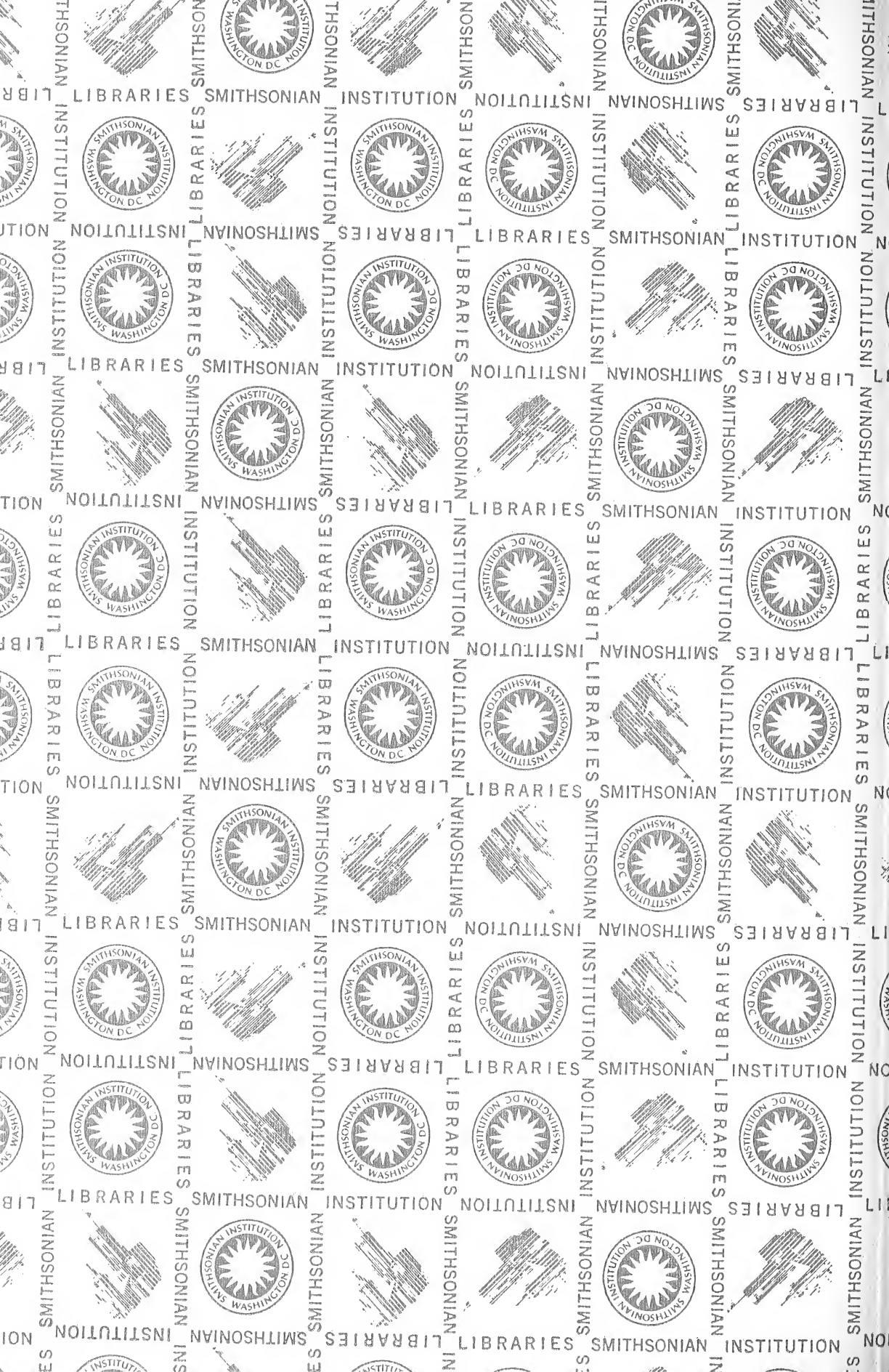
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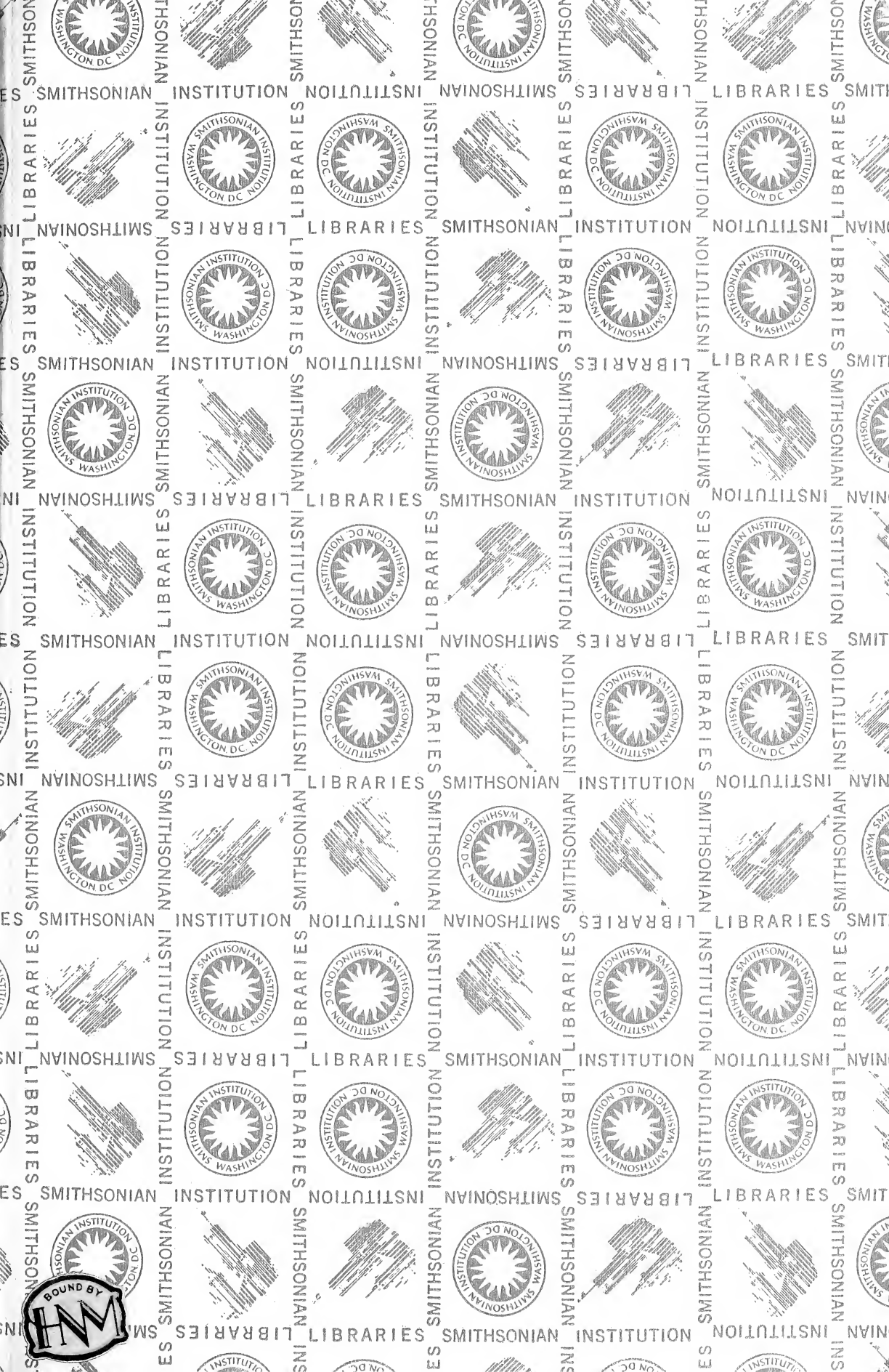
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